

Age-Related Characteristics of Foraging Habitats and Foraging Behaviors in the Black Phoebe (*Sayornis nigricans*)

Author(s): Megan D. Gall , Leah D. Hough , and Esteban Fernández-Juricic

Source: The Southwestern Naturalist, 58(1):41-49. 2013.

Published By: Southwestern Association of Naturalists

DOI: <http://dx.doi.org/10.1894/0038-4909-58.1.41>

URL: <http://www.bioone.org/doi/full/10.1894/0038-4909-58.1.41>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

AGE-RELATED CHARACTERISTICS OF FORAGING HABITATS AND FORAGING BEHAVIORS IN THE BLACK PHOEBE (*SAYORNIS NIGRICANS*)

MEGAN D. GALL,* LEAH D. HOUGH, AND ESTEBAN FERNÁNDEZ-JURICIC

Department of Biological Sciences, Purdue University, West Lafayette, IN 47907 (MDG, EFJ)

Department of Biological Sciences, California State University Long Beach, Long Beach, CA 90840 (LDH)

**Correspondent: mgall@purdue.edu*

ABSTRACT—We studied how age affects selection of foraging microhabitats, foraging behaviors, and rates of vigilance in the black phoebe (*Sayornis nigricans*). Juveniles generally perched higher in trees than adults and in areas with higher intensity of light, which may increase the difficulty of visually tracking prey. Juveniles allocated more effort to visual searching prior to a foraging attempt and flew farther than adults to capture a prey item. When at rest on a perch, juveniles monitored the environment more slowly than adults, suggesting lower levels of vigilance. In general, our results suggest that differences between ages in foraging behavior of visually guided predators may be influenced by intensity of ambient light in their foraging territories.

RESUMEN—Estudiamos como la edad afecta la selección de microhábitats de forrajeo, el comportamiento de forrajeo, y las tasas de vigilancia del mosquero negro (*Sayornis nigricans*). Los juveniles se hallaron en perchas más altas en los árboles que los adultos y en áreas con mayor intensidad de luz, lo que puede aumentar la dificultad de rastrear visualmente a la presa. Los juveniles asignaron un esfuerzo mayor a la búsqueda visual de presa antes de un intento de depredación y se desplazaron una distancia mayor para capturar a las presas que los adultos. Cuando descansaron en una percha, los juveniles monitorearon el entorno más lentamente que los adultos, lo que sugiere niveles menores de vigilancia. En general, nuestros resultados sugieren que las diferencias de edad en el comportamiento de alimentación de predadores visuales están influenciadas por la intensidad de luz en sus territorios de forrajeo.

A key trade-off exists between the energetic benefit of obtaining a food item and the risk of predation (Lima and Dill, 1990). Foraging-predation optima are likely to differ between age classes because juveniles often allocate more time to foraging and are less successful than adults (Breitwisch et al., 1987; Desrochers, 1992; Vanderhoff and Eason, 2008). Concomitantly, foraging-predation optima may differ between age classes because juveniles may react more fearfully (Rajala et al., 2003; Hollén and Radford, 2009) or spend less time engaged in vigilance or anti-predator behaviors than adults (Arenz and Leger, 2000; Boukhriss et al., 2007; Hollén et al., 2008).

The difference in foraging-vigilance optima between age classes may be particularly pronounced in species that forage on prey that move rapidly in three-dimensional space (Marchetti and Price, 1989) and this requires complex foraging behavior such as hawking of flying insects (Davies, 1976), plunge-diving (Burger and Gochfeld, 1983), or foraging near large ungulates (Burger and Gochfeld, 1989). To successfully capture these prey items, individuals must accurately track and determine the location of capture, which requires greater foraging experience (Burger and Gochfeld, 1983; Marchetti and

Price, 1989) and more complicated sensory processing than capturing stationary food items (e.g., depth perception through motion parallax; Land, 1999). In these species, foraging and vigilance behavior are tied closely to microhabitat not only because microhabitats differ in abundance of predators, prey, and conspecific competitors (Moyle, 1966; Maccarone, 1987; Marchetti and Price, 1989; Wagner and Gauthreaux, 1990; Cresswell, 1994; Brotons et al., 2000) but also because the visual environment (e.g., color and intensity of light, as well as physical structure of habitat) influences the ability to acquire sensory information (Bradbury and Vehrenkamp, 1998).

We investigated characteristics of foraging habitat, foraging behavior, and vigilance (e.g., rates of movement of head) in juvenile and adult black phoebes (*Sayornis nigricans*). Black phoebes are small sit-and-wait flycatchers that forage on prey items that move rapidly in three-dimensional space. Previous research determined that foraging behavior of adult black phoebes, including searching for prey, is influenced by light and the physical structure of foraging habitats (Gall and Fernández-Juricic, 2009). Juvenile black phoebes forage independently

within 24 h of leaving the nest, often in patches of habitat adjacent to adults (Oberlander, 1939). However, foraging competence is expected to take a long time to develop because it may be difficult to track and determine the location of capture for prey moving in three-dimensional space. Therefore, we expected that juveniles would select patches of habitat that would enhance visual access to prey, at the possible expense of increasing risk of predation, allocate more effort to foraging than adults, and be less vigilant than adults because of trade-offs between foraging and vigilance.

Black phoebes have been increasing in abundance in urban environments in recent decades (Wolf, 1997). Successful urban species have high rates of feeding innovation, high annual fecundity, and high survivorship of adults (Møller, 2009). However, fledging success may be reduced in these species because of lower availability of natural food (Chamberlain et al., 2009). Therefore, understanding factors influencing foraging behavior of juvenile and adult flycatchers also can provide insights into behavioral mechanisms of use of habitats by flycatchers in urban environments.

MATERIALS AND METHODS—We conducted our study in 15 urban parks and on college campuses in Los Angeles County and Orange County, California. Study areas were bounded on all sides by an urban or suburban matrix of housing and retail establishments. Study areas had similar vegetation, with large areas of nonnative grasses and a combination of sparsely distributed native and nonnative trees. Study areas frequently were used by humans, but varied in degree and temporal patterns of use. Black phoebes have been highly successful in urban areas, due in part to expansion of suitable nesting locations provided by human-made structures (Wolf, 1997). In our study areas, black phoebes were highly habituated to humans and could be approached to a distance of <5 m without flushing, although we always remained ≥ 15 m from individuals.

We sampled a total of 58 individuals (37 adults and 21 juveniles) during March–May 2007 to address whether juveniles and adults differed in structure of microhabitats used for foraging, microclimates of foraging patches, and foraging behaviors. We used a subset of 38 individuals (20 adults and 18 juveniles) to determine if juveniles and adults differed in visual scanning. Because 20 birds engaged in frequent foraging sallies, we were unable to measure visual scanning when these individuals were at rest on a perch. We did not band individuals, but territorial behavior of the black phoebes and our sampling procedure minimized the chances of pseudoreplication. In the breeding season, territories are small (0.5–0.8 ha; Wolf, 1997). Therefore, small parks (<2 ha) were visited on 1 day only and only 1–2 individuals were sampled to ensure that we would not use the same individual more than once. In large parks and on college campuses (>2 ha), we sampled adults that were separated by ≥ 0.5 km to minimize the chances of pseudoreplication. We did not sample juveniles in large parks on >1 day.

We choose sampling locations within each park by choosing a compass direction and number of paces to walk from a random-number table. Once we encountered an individual, we followed

it until it alighted on a perch. We maintained a distance of ≥ 15 m from the individual during observations. We then used a Canon ZX50 digital video camera (Canon USA, Inc., Lake Success, New York) to record the individual on the perch until it initiated a foraging flight. Foraging flights were identified visually by their highly stereotyped shape and acoustically by bill snaps that occurred when an insect was captured. If an individual engaged in other types of flight (e.g., changing patches), we followed the individual to the new location and continued to record it until a foraging flight was completed. We recorded only one foraging flight from each individual. From the videos, we determined whether an individual was a juvenile or adult based on color of bill and wing bars following Wolf (1997). Videos also were used to assess visual searching for food and vigilance.

After the foraging flight, we measured height of the perch and tree the individual used. Height of tree was measured by having one observer stand far enough from the tree that the observer could visually align a ruler with the top and bottom of the tree. That observer then rotated the ruler 90° so the ruler was aligned with the ground and perpendicular to the tree, effectively projecting the height of the tree onto the ground. A second person marked the endpoint of this projection with a flag. We then measured the projected height of the tree (i.e., distance along the ground from base of tree to the flag) with a meter tape as described by Fernández-Juricic et al. (2005). We used the same procedure to determine height of perch. Measurements of height of perch were corroborated with a meter tape when the perch was <2 m in height. We measured percentage cover of grasses following Prodon and Lebetron (1981) and number of trees within a 10-m radius of the perch, which is the upper limit of length of foraging flights (Gall and Fernández-Juricic, 2009). We used an Extech Instruments Lux Meter (model 401025; Extech Instruments, Waltham, Massachusetts) to measure intensity of light at the perch and a Speedtech Skymaster (model SM-28; Speedtech, Great Falls, Virginia) to record temperature and humidity.

After an individual made a foraging sally, we immediately marked the ground directly below the location of capture (prey generally were captured in the air) with a plastic marker. Location and height of capture was determined in the field by consensus of two observers and consultation with the foraging video. We then measured height of the location of capture and linear distance from perch to site of capture with a meter tape. We also measured length of flight path, taking into account both the vertical and horizontal distance traveled from the perch to site of capture. Intensity of light at site of capture was measured with an Extech Instruments Lux Meter.

We used JWatcher version 1.0 (Blumstein and Daniel, 2007) to measure rate of movement of the head immediately preceding a foraging flight, length of pre-foraging movement of head (i.e., the amount of time an individual spent rapidly moving its head prior to initiating a foraging attempt), and background rate of movement of the head (i.e., number of movements of the head per second when individuals were at rest on a perch) from the videos following Gall and Fernández-Juricic (2009). For the background rate of movement of the head, we analyzed 30 s of video with a start time chosen using a random-number table.

All data were checked for normality and homoscedasticity. Transformations were chosen using the Box-Cox procedure in

TABLE 1—Canonical weights, canonical coefficients, and descriptive statistics for dependent variables of microhabitat with age of black phoebes (*Sayornis nigricans*) as an independent variable. Descriptive statistics for adults and juveniles are back-transformed least-squares means with 95% confidence intervals in parentheses.

Dependent variable	Canonical weight	Standardized canonical coefficient	Adults	Juveniles
Structure of microhabitat				
Number of trees	-0.26	-1.06	1.7 (1.3, 2.3)	1.1 (0.8, 1.6)
Cover by grasses (%)	-0.08	-1.35	61.6 (39.8, 83.4)	50.6 (33.2, 67.9)
Height of tree (m)	0.16	-4.02	2.6 (0.7, 10.1)	5.7 (1.0, 31.2)
Height of perch (m)	0.55	5.72	1.3 (0.7, 2.4)	3.0 (1.4, 6.5)
Microclimate of foraging patch				
Temperature (°C)	0.84	1.36	20.2 (19.0, 21.4)	21.9 (20.3, 23.5)
Humidity (%)	-0.41	-0.04	54.4 (48.5, 60.3)	51.4 (43.7, 59.2)
Intensity of light at perch (lux)	0.70	1.04	248.1 (164, 239.6)	378.2 (242, 544.6)

PROC TRANSREG in SAS 9.2 (SAS Institute, Inc., Cary, North Carolina) for all variables that did not meet the assumptions. We conducted three MANOVAs in PROC GLM with the CANONICAL option to assess whether juveniles and adults differed in their selection of structure of microhabitats, microclimate of the foraging patch, and foraging behavior with age as an independent variable. Here, the two age classes were represented by a dummy variable (juvenile = 0 and adults = 1). We choose a MANOVA with the CANONICAL option because it allowed us to include date and time as random variables in the model. The CANONICAL option for a MANOVA in PROC GLM creates an axis that maximizes correlation between a linear combination of dependent and independent variables. Here, canonical weights can be interpreted as Pearson’s correlation coefficients and represent the strength of the association between the original variable and the canonical variate. Canonical coefficients are equivalent to the slope of the relationship between the original variable and the canonical variate when all other variables are held constant. Standardized canonical coefficients were calculated after each variable had been transformed to have a mean of 0 and a standard deviation of 1, allowing the coefficients to be directly compared, regardless of magnitude of the original variables. The term canonical weight is sometimes used synonymously with canonical coefficient, but that is not the case here.

Time of day and date were included as random factors because our sampling efforts were concentrated on a relatively small number of days. Dependent variables in the model of microhabitat were height of tree (log-transformed), height of perch (log-transformed), percentage cover of grasses, and number of trees (log-transformed) within 10 m of the perch. In the model analyzing microclimate of the foraging patch, dependent variables were temperature, humidity, and intensity of light at the perch (square-root transformed). Dependent variables in the model of foraging behavior were height of capture (1/square-root transformed), intensity of light at site of capture (square-root transformed), linear distance of site of capture from the perch (square-root transformed), length of flight path (log-transformed), angle of flight (square-root transformed), rate of movement of head, and length of head-moving bout (log-transformed). When we encountered potential multicollinearity, we also conducted univariate ANOVAs in PROC GLM. Background scanning was examined with an

ANOVA in PROC GLM. Rate of movement of head was the only dependent variable in the visual-scanning model.

RESULTS—A MANOVA revealed an overall difference in structure of foraging microhabitats between juvenile ($n = 21$) and adult ($n = 37$) black phoebes (Wilks’ $\lambda = 0.2$, $F_{4,6} = 5.99$, $P = 0.03$). Age explained 80% of variation in the multivariate model, with a canonical correlation coefficient of 0.89 between age and the dependent canonical variate. Juveniles had higher scores on canonical variates than adults. Number of trees and percentage cover of grasses were correlated negatively with the canonical variate (canonical weight), while height of tree and height of perch were correlated positively with the canonical variate (Table 1; Fig. 1). Height of perch and number of trees had the greatest canonical weight, suggesting they contribute most strongly to the canonical variate (Table 1). Standardized canonical coefficients were negative for number of trees, percentage cover of grasses and height of tree (Table 1). The standardized canonical coefficient was positive for height of perch. Magnitude of the canonical coefficient was greatest for height of perch, suggesting this variable is the most important in determining scores on the canonical variate. These results suggest that in a multivariate context juveniles perched higher than adults. Juveniles also foraged from taller trees and in areas with fewer trees and less grass, although these factors did not weight as strongly as height of perch.

There was no multivariate difference between juveniles ($n = 21$) and adults ($n = 37$) in microclimate of foraging patch (Wilks’ $\lambda = 0.83$, $F_{3,16} = 1.13$, $P = 0.37$). All three dependent variables were correlated strongly with the canonical variate, suggesting they all contributed strongly to the canonical variate (Table 1). Temperature and intensity of light at perch were correlated positively with the canonical variate (Table 1; Figs. 2a and 2c), and humidity was correlated negatively with the canonical variate (Table 1; Fig. 2b). Temperature and humidity were correlated strongly with each other ($r = -0.83$, $P <$

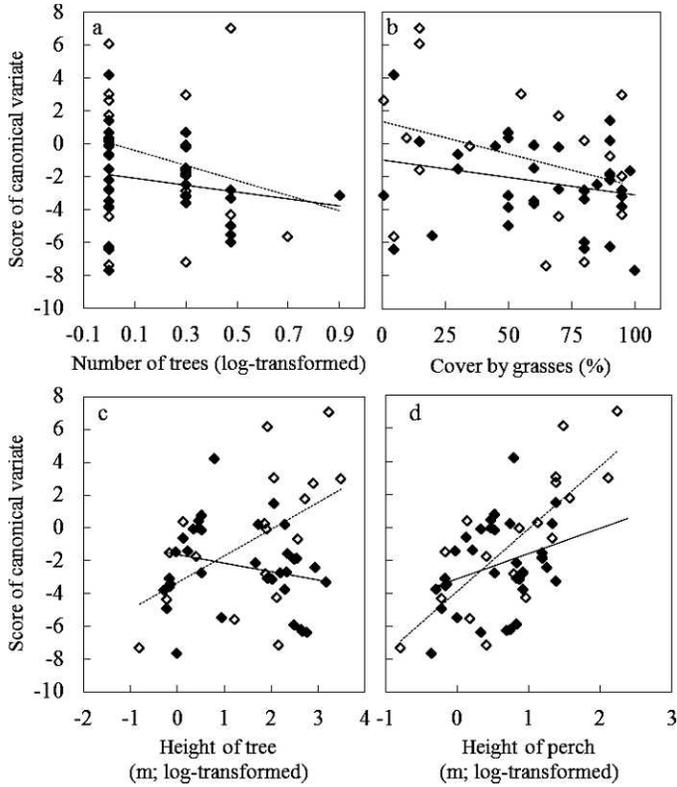


FIG. 1—Scores on canonical variates plotted against the original dependent variables from the MANOVA of microhabitat as a function of age of black phoebes (*Sayornis nigricans*): a, number of trees (log-transformed); b, cover by grasses (%); c, height of trees (m; log-transformed); d, height of perch (m; log-transformed). Juveniles (.....◇.....) had higher scores on canonical variates than adults (—◆—). Age explained 80% of variation in canonical scores when time of day and date were included as random factors in the model.

0.001). Intensity of light was not correlated strongly with temperature ($r = 0.22, P = 0.09$) or humidity ($r = -0.17, P = 0.18$). Univariate analyses suggested that juveniles forage from perches with higher intensity of light than adults ($F_{1,39} = 2.46, P = 0.02$), but that there was no difference in temperature ($F_{1,39} = 0.74, P = 0.42$) or humidity ($F_{1,39} = 1.5, P = 0.17$) of these perches.

There was an overall difference in foraging behavior between juvenile ($n = 21$) and adult ($n = 37$) black phoebes (Wilks' $\lambda = 0.28, F_{7,12} = 4.5, P = 0.02$). Age explained 72% of variation in the multivariate model, with a canonical correlation coefficient of 0.85 between the independent variable and the canonical variate. Juveniles had higher scores on canonical variates than adults. All dependent variables had positive canonical weights except for distance of capture from the perch (Table 2; Fig. 3). Note that height of capture was inverse-transformed, so direction of the relationship for the untransformed variable would be opposite of what is seen here. Rate of movement of head and length of flight path had the highest canonical weights, suggesting they were the most important factors in the canonical variate (Table 2). Distance from perch and height of capture had lowest canonical weights and, therefore, did not explain much variation in the canonical variate (Table 2). Intensity of light at site of capture, length of head-moving bout, rate of movement of head, height of capture, and length of flight path had positive standardized canonical coefficients, while angle of flight and distance from perch had negative canonical coefficients (Table 2). An angle of flight of 90° is parallel to the ground and 0° is perpendicular to the ground. Length of flight path had a large standardized canonical coefficient, suggesting it

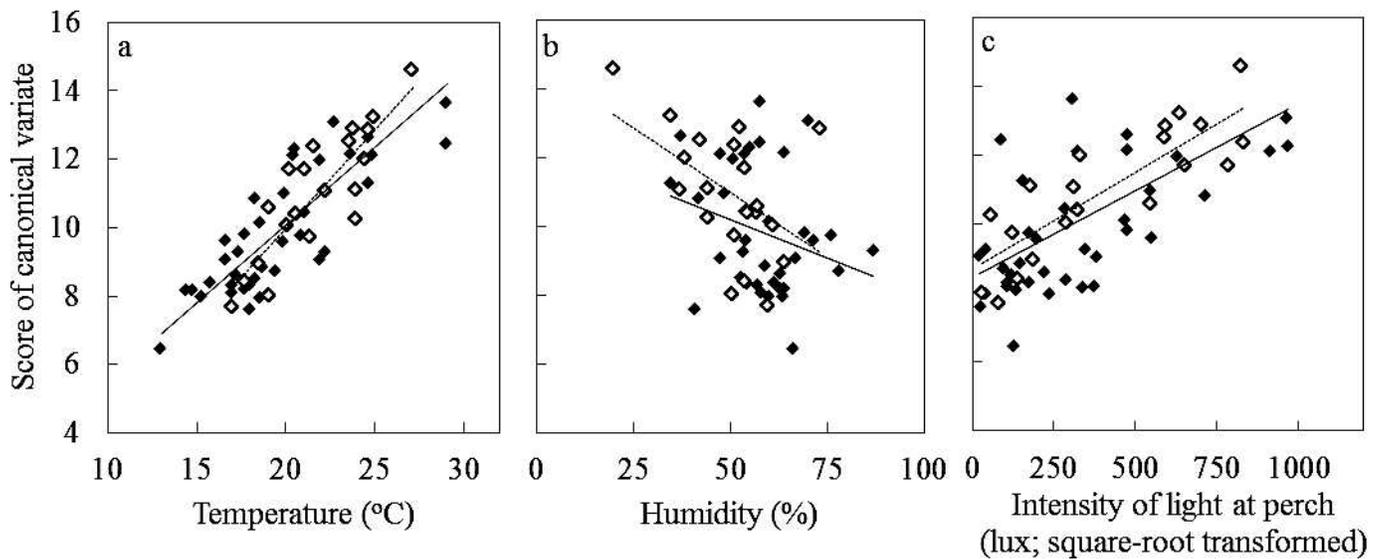


FIG. 2—Scores on canonical variates for microclimate of foraging patches as a function of age of black phoebes (*Sayornis nigricans*) plotted against the original dependent variables from the MANOVA: a, temperature ($^\circ\text{C}$); b, humidity (%); c, intensity of light at perch (lux). There was no difference between juveniles (.....◇.....) and adults (—◆—) in scores on canonical variates when time of day and date were included as random factors in the model.

TABLE 2—Canonical weights, canonical coefficients, and descriptive statistics for dependent variables of foraging with age of black phoebes (*Sayornis nigricans*) as an independent variable. Descriptive statistics for adults and juveniles are back-transformed least-squares means with 95% confidence intervals in parentheses.

Dependent variable	Canonical weight	Standardized canonical coefficient	Dependent variable	
			Adults	Juveniles
Intensity of light at site of capture (lux)	0.23	0.32	324.9 (230.5, 435.5)	383.1 (250.3, 544.2)
Length of head-movement bout (s)	0.14	0.53	14.6 (8.6, 24.8)	18.8 (9.36, 37.8)
Rate of movement of head (s ⁻¹)	0.32	0.96	0.9 (0.8, 1.0)	1.1 (1.0, 1.3)
Distance from perch (m)	-0.04	-4.36	5.0 (3.3, 7.0)	4.6 (2.6, 7.3)
Height of capture (m)	0.06	0.53	1.7 (0.9, 3.7)	1.2 (0.7, 3.2)
Angle of flight (degrees)	0.23	-1.10	18.6 (9.4, 30.8)	27.9 (13.3, 47.9)
Length of flight path (m)	0.32	4.21	4.5 (3.4, 5.9)	6.5 (4.5, 9.3)

contributed strongly to scores of canonical variates. These results suggest that when considered in a multivariate context, juveniles generally scanned more rapidly before a foraging flight and had longer flight paths than adults. Juveniles also had greater angles of flight (i.e., flights were not as steep) and foraged in brighter areas than adults. Juveniles spent more time scanning (length of head-moving bout), did not fly as far from the perch (linear distance of flight), and caught prey lower in the air than adults; however, these factors did not weight strongly in the model and are likely to be less important than other factors. When resting on a perch, juveniles (0.72 ± 0.05 movements of head/s, $n = 18$) visually monitored their environment at a significantly slower rate than adults (0.85 ± 0.05 movements of head/s, $n = 20$; $F_{1,36} = 4.71$, $P = 0.04$).

DISCUSSION—Juvenile black phoebes differed from adults in characteristics of foraging microhabitats, foraging behaviors, and scanning behaviors. Juveniles perched higher in trees and in areas with higher intensity of light than adults. Juveniles moved their heads faster, for a longer time prior to initiating a foraging flight, and caught prey at sites with higher ambient intensity of light than adults. Juveniles had longer flight paths, likely due to perching higher in trees, which could lead to juveniles being less efficient over multiple foraging attempts, as reported in other taxa (Gochfeld and Burger, 1984; Marchetti and Price, 1989; Jansen and Van Schaik, 2002; Heise and Moore, 2003). Finally, juveniles scanned their environment with fewer movements of the head than adults when at rest on a perch. Although we did not design our study to identify mechanisms responsible for these differences, we propose at least four nonmutually exclusive potential explanations for patterns we observed; inexperience of juveniles or their displacement by adults, systematic seasonal changes, ontogenetic differences in the visual system, and differences in the visual environment that juveniles and adults occupied.

Juveniles were in habitats with characteristics that generally were avoided by adults and resulted in greater investments in visual searching. Previously, we detected that adult black phoebes preferred perches that had

lower intensity of light than random perches in the environment (Gall and Fernández-Juricic, 2009). In a variety of taxa, juveniles are excluded from preferred patches by adults (Sherry and Holmes, 1989; Brotons et al., 2000), which could result in juveniles perching in areas with higher intensity of light. This displacement could lead to juveniles foraging in less-productive areas in terms of availability of food or more dangerous areas in terms of exposure to predators, which could lead to changes in foraging or antipredator behavior (Koivula et al., 1994; Sol et al., 2000). An alternative interpretation is that juveniles lack the experience needed to select a proper foraging site, to forage efficiently, or to engage in appropriate scanning behavior (Weathers and Sullivan, 1991). For instance, young spotted flycatchers (*Muscicapula striata*) capture small, slow-moving prey, presumably because they are easier to catch (Davies, 1976), suggesting juveniles may be more limited in the prey they can successfully capture due to inexperience. Juveniles put more visual effort into foraging than adults, which could come at the expense of antipredator vigilance. Juveniles of many species appear to have lower vigilance than adults or engage in riskier behavior than adults (East, 1986; Arenz and Leger, 2000) due to inexperience with predators.

Systematic seasonal changes in behavior or characteristics of habitat also could produce differences between adults and juveniles. However, we believe this possibility is unlikely, as timing of our sampling of adults and juveniles overlapped substantially and we controlled for date statistically. It also is possible that differences in characteristics of foraging habitats may arise if juveniles are overrepresented in habitats where nesting success is high. Although we did not map territories of individuals, juveniles and adults were relatively close to one another in large parks and were frequently in adjacent sampling areas. Moreover, characteristics of habitats selected by juveniles were determined previously to result in diminished visual and physical access to prey (Gall and Fernández-Juricic, 2009). This suggests that juveniles were in foraging habitats that were less productive than those of adults and unlikely to result in higher nesting success.

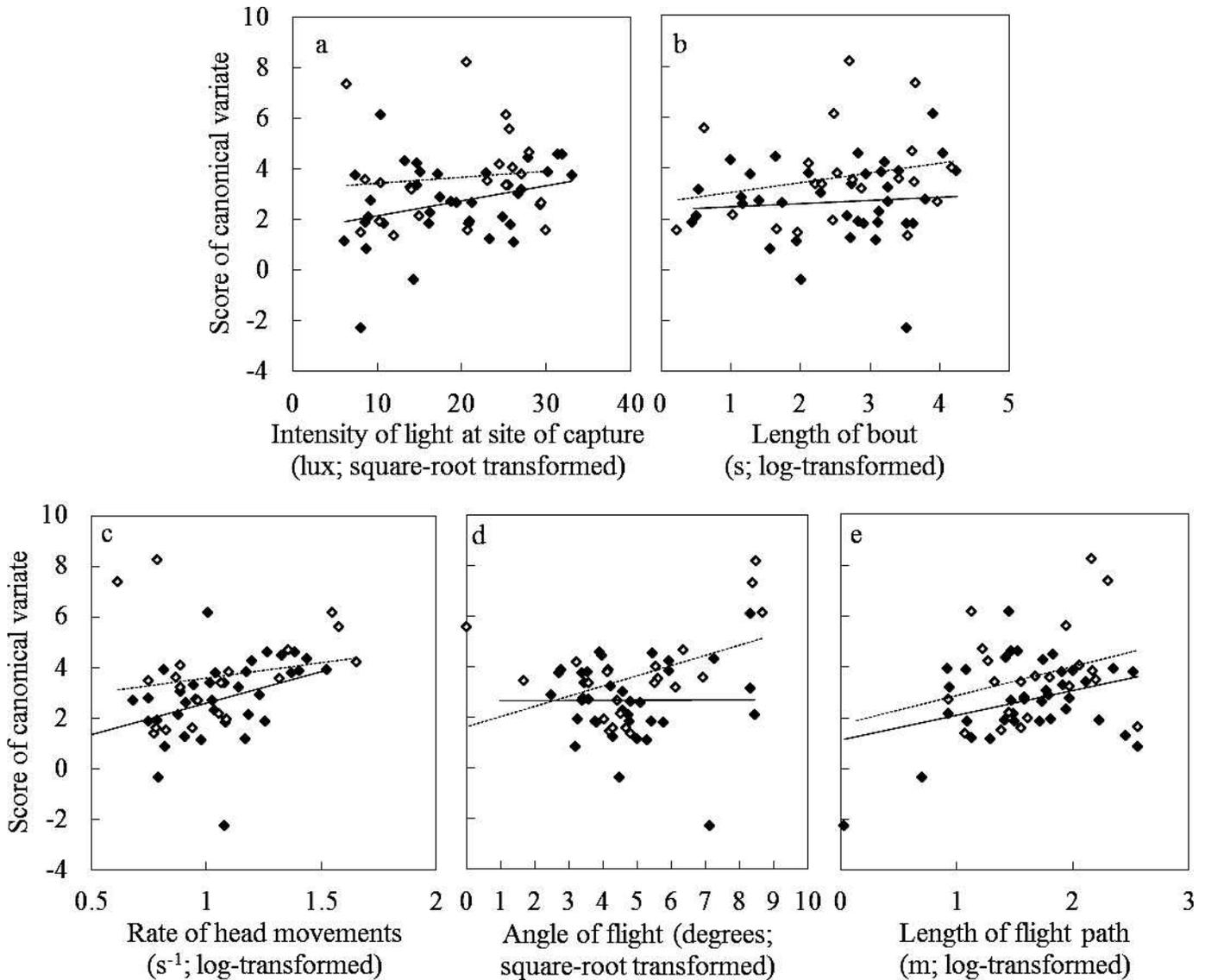


FIG. 3—Scores on canonical variates for foraging as a function of age of black phoebes (*Sayornis nigricans*) plotted against the original dependent variables from the MANOVA: a, intensity of light at site of capture (lux); b, log length of bout (s); c, rate of movement of head (s^{-1}); d, angle of flight (degrees); e, log length of flight path (m). Juveniles (.....◇.....) had higher scores on canonical variates than adults (—◆—). Age explained 72% of variation in canonical scores when time and date were included as random factors in the model.

Differences between visual systems of juveniles and adults also could result in selection of different microhabitats, as well as different foraging and scanning behaviors. Sensory and motor neural pathways can be influenced by experience (e.g., training; Feldman and Knudsen, 1997) and ontogenetic factors (Dmitrieva and Gottlieb, 1992; Schaeffel and Wagner, 1996; Brittan-Powell et al., 2004). For instance, in barn owls (*Tyto alba*), visual experience tunes the map of auditory space in the inferior colliculus (Feldman and Knudsen, 1997), which can improve ability to locate prey. The visual cortex also can be altered by visual experience and cortical plasticity is greater in juveniles than in adults (Medini and Pizzorusso, 2008). Additionally, morphology of eyes can

change with ontogeny. For example, diameter of pupil, axial length of eye, and size of anterior chamber of the eye can continue to increase after fledging (Schaeffel and Wagner, 1996), which can lead to improved quality of images. If juveniles do not have a fully developed visual system (e.g., smaller eyes, comparatively lower visual acuity), visual tasks, such as locating a prey item, may take more effort. This would be expected to result in faster movements of the head prior to a foraging flight to increase the amount of information gathered from the environment, as detected in our study. Moving the head faster may allow individuals of a species with laterally placed eyes to quickly track an object with the right and left foveae (Gall and Fernández-Juricic, 2010). Alterna-

tively, differences in the visual environment of adults and juveniles may influence differences in ages in foraging behavior and visual monitoring. High ambient-light conditions can reduce use of foraging patches, food-seeking behavior, and delay detection of predators by house finches (*Carpodacus mexicanus*), possibly as a result of higher thermal stress, greater visual exposure to predators, and effects of glare in reducing visual contrast between the object and the background (Fernández-Juricic and Tran, 2007). Juvenile black phoebes perched and caught prey at sites with higher ambient-light intensity than perches and locations where adults were captured, which may require more visual effort to locate and track prey.

Studies of foraging behavior and selection of microhabitats generally have focused on animals living in native or pristine habitats (Sherry and Holmes, 1989; Cresswell, 1994; Brotons et al., 2000; Heise and Moore, 2003). However, urban environments can be quite diverse in terms of composition of native avian species (Pautasso et al., 2011). Therefore, understanding characteristics of foraging sites and development of foraging behavior in native species of birds can allow us to better understand the process of colonization and persistence in urban areas. Survival of juveniles is particularly important for viability of urban populations; therefore, it is necessary to have an understanding of characteristics of their foraging habitat and behavior. This can allow habitat managers to increase local biodiversity of birds by providing suitable foraging opportunities for adults and juveniles.

The black phoebe is a particularly good model of a native specialist colonizing urban environments. Generally, urban environments favor granivores and limit species that forage primarily on arthropods (Kark et al., 2007). In California, many native insectivorous birds have been impacted negatively by urban sprawl (e.g., California gnatcatcher *Poliophtila californica*; Akçakaya and Atwood, 1997), while populations of black phoebes have not only persisted, but increased in numbers and spatial extent in urbanized areas. Black phoebes traditionally inhabited riparian areas where nesting sites were limited. Urban development and human-made structures have increased the number of suitable nesting areas and foraging areas, likely facilitating expansion of populations (Wolf, 1997). An abundance of suitable nesting and foraging areas may be particularly important, as urban populations often have lower nesting productivity than non-urban populations, which may be linked to availability of food or to predation (Chamberlain et al., 2009). Conversely, in some species, rates of predation on juveniles appear to be lower in highly urbanized habitats (Whittaker and Marzluff, 2009). This may be particularly important for juvenile black phoebes, as foraging in open areas tends to increase the risk of predation in passerines (Lima, 1993). Juvenile black phoebes may be able to offset this risk somewhat by perching higher and in taller trees than adults. However,

this may come at the expense of longer flight paths during foraging attempts.

Anecdotally, we found that, like adults, juvenile black phoebes successfully captured a prey item in >95% of foraging attempts. Therefore, availability of food in urban areas and the effort expended during each foraging attempt, rather than success in captures may drive foraging efficiency in juveniles. It would be particularly valuable to know if foraging behavior and abundance of black phoebes is affected by pesticides and watering regimes in urban parks and on college campuses, as this could dramatically affect suitability of a foraging area. Moreover, it would be valuable to know if urban areas provide greater or more consistent food resources than native habitats.

Juvenile black phoebes have different strategies for foraging and in selection of microhabitats than adults in urbanized areas. Although our experimental design did not allow us to tease apart specific mechanisms behind this difference, our results suggest the possibility that the visual environment may influence differences in age in foraging strategies. Expanding our understanding of ontogenetic changes in visual physiology of passerine birds and how visual systems with different developmental stages may perform in different ambient light conditions may illuminate the mechanistic basis of differences among ages in foraging and vigilance.

We thank K. Henry, M. Nolen, L. Brierley, J. Randolet, P. Baumhardt, J. Lucas, and anonymous reviewers for feedback on an early version of the manuscript. We also thank S. Thomas and J. Caprile for assistance in collection of data. This work was supported by a Sigma Xi Grant-In-Aid of Research.

LITERATURE CITED

- AKÇAKAYA, H. R., AND J. L. ATWOOD. 1997. A habitat-based metapopulation model of the California gnatcatcher. *Conservation Biology* 11:422–434.
- ARENZ, C. L., AND D. W. LEGER. 2000. Antipredator vigilance of juvenile and adult thirteen-lined ground squirrels and the role of nutritional need. *Animal Behaviour* 59:535–541.
- BLUMSTEIN, D. T., AND J. C. DANIEL. 2007. Quantifying behavior the JWitcher way. Sinauer Associates, Sunderland, Massachusetts.
- BOUKHRISS, J., S. SELMI, A. BÉCHET, AND S. NOUIRA. 2007. Vigilance in greater flamingos wintering in southern Tunisia: age-dependent flock size effect. *Ethology* 113:377–385.
- BRADBURY, J. W., AND S. L. VEHERNCAMP. 1998. Principles of animal communication. Sinauer Associates, Sunderland, Massachusetts.
- BREITWISCH, R., M. DIAZ, AND R. LEE. 1987. Foraging efficiencies and techniques of juvenile and adult northern mockingbirds *Mimus polyglottos*. *Behaviour* 101:225–235.
- BRITTAN-POWELL, E. F., R. J. DOOLING, AND O. GLEICH. 2004. Development of auditory sensitivity in budgerigars *Melopsittacus undulatus*. *Journal of the Acoustical Society of America* 115:3092–3102.
- BROTONS, L., M. ORELL, K. LAHTI, AND K. KOIVULA. 2000. Age-

- related microhabitat segregation in willow tit *Parus montanus* winter flocks. *Ethology* 106:993–1005.
- BURGER, J., AND M. GOCHFELD. 1983. Feeding behavior in laughing gulls: site selection by young. *Condor* 85:467–473.
- BURGER, J., AND M. GOCHFELD. 1989. Age differences in cattle egrets *Bubulcus ibis*, foraging with wild ungulates in Kenya. *Ardea* 77:201–204.
- CHAMBERLAIN, D. E., A. R. CANNON, M. P. TOMS, D. I. LEECH, B. J. HATCHWELL, AND K. J. GASTON. 2009. Avian productivity in urban landscapes: a review and meta-analysis. *Ibis* 151:1–18.
- CRESSWELL, W. 1994. Age-dependent choice of redshank (*Tringa tetanus*) feeding location: profitability or risk? *Journal of Animal Ecology* 63:589–600.
- DAVIES, N. B. 1976. Parental care and the transition to independent feeding in the young spotted flycatcher (*Muscicapa striata*). *Behaviour* 59:280–295.
- DESROCHERS, A. 1992. Age and foraging success in European blackbirds: variation between and within individuals. *Animal Behaviour* 43:885–894.
- DMITRIEVA, L. P., AND G. GOTTLIEB. 1992. Development of brainstem auditory pathway in mallard duck embryos and hatchlings. *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 171:665–671.
- EAST, M. 1986. Crop selection, feeding skills and risks taken by adult and juvenile rooks *Corvus frugilegus*. *Ibis* 130:294–299.
- FELDMAN, D. E., AND E. I. KNUDSEN. 1997. An anatomical basis for visual calibration of the auditory space map in the barn owl's midbrain. *Journal of Neuroscience* 17:6820–6837.
- FERNÁNDEZ-JURICIC, E., AND E. TRAN. 2007. Changes in vigilance and foraging behavior with light intensity and their effects on food intake and predator detection in house finches. *Animal Behaviour* 74:1381–1390.
- FERNÁNDEZ-JURICIC, E., R. POSTON, K. DE COLLIBUS, T. MORGAN, B. BASTAIN, C. MARTIN, K. JONES, AND R. TREMINIO. 2005. Microhabitat selection and singing behavior patterns of male house finches (*Carpodacus mexicanus*) in urban parks in a heavily urbanized landscape in the western U.S. *Urban Habitats* 3:49–69.
- GALL, M. D., AND E. FERNÁNDEZ-JURICIC. 2009. Physical and visual access to prey modifies patch selection and food search effort in a sit-and-wait predator, the black phoebe. *Condor* 111:150–158.
- GALL, M. D., AND E. FERNÁNDEZ-JURICIC. 2010. Visual fields, eye movements, and scanning behavior of a sit-and-wait predator, the black phoebe (*Sayornis nigricans*). *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 196:15–22.
- GOCHFELD, M., AND J. BURGER. 1984. Age differences in the foraging behavior of the American robin (*Turdus migratorius*). *Behaviour* 88:227–239.
- HEISE, C. D., AND F. R. MOORE. 2003. Age-related differences in foraging efficiency, molt, and fat deposition of gray vatsbirds prior to autumn migration. *Condor* 105:496–504.
- HOLLÉN, L. I., AND A. N. RADFORD. 2009. The development of alarm call behavior in mammals and birds. *Animal Behaviour* 78:791–800.
- HOLLÉN, L. I., T. CLUTTON-BROCK, AND M. B. MASER. 2008. Ontogenetic changes in alarm-call production and usage in meerkats (*Suricata suricatta*): adaptations or constraints? *Behavioral Ecology and Sociobiology* 62:821–829.
- JANSON, C. H., AND C. P. VAN SCHAIK. 2002. Ecological risk aversion in juvenile primates: slow and steady wins the race. Pages 57–85 in *Juvenile primates: life history, development, and behavior* (M. E. Pereira and L. A. Fairbanks, editors). Oxford University Press, New York.
- KARK, S., A. IWANIUK, A. SCHALIMITZEK, AND E. BANKER. 2007. Living in the city: can anyone become an 'urban exploiter'? *Journal of Biogeography* 34:638–651.
- KOIVULA, K., K. LAHTI, S. RYTKONEN, AND M. ORELL. 1994. Do subordinates expose themselves to predation? Field experiments on feeding site selection by willow tits. *Journal of Avian Biology* 25:178–183.
- LAND, M. F. 1999. The roles of head movements in the search and capture strategy of a tern (Aves, Laridae). *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 184:265–272.
- LIMA, S. L. 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *Wilson Bulletin* 105:1–47.
- LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- MACCARONE, A. D. 1987. Age-class differences in the use of food sources by European starlings. *Wilson Bulletin* 99:699–704.
- MARCHETTI, K., AND T. PRICE. 1989. Differences in the foraging of adult and juvenile birds: the importance of developmental constraints. *Biological Review* 64:51–70.
- MEDINI, P., AND T. PIZZORUSSO. 2008. Visual experience and plasticity of the visual cortex: a role for epigenetic mechanisms. *Frontiers in Bioscience* 13:3000–3007.
- MØLLER, A. P. 2009. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the western Palearctic. *Oecologia* (Berlin) 159:849–858.
- MOYLE, P. 1966. Feeding behavior of the glaucous-winged gull on an Alaskan salmon stream. *Wilson Bulletin* 78:175–190.
- OVERLANDER, G. 1939. The history of a family of black phoebes. *Condor* 41:133–151.
- PAUTASSO, M., K. BÖHNING-GAESE, P. CLERGEAU, V. R. CUETO, M. DINETTI, E. FERNÁNDEZ-JURICIC, M. L. KAISANLAHTI-JOKIMÄKI, J. JOKIMÄKI, M. L. MCKINNEY, N. S. SODHI, D. STORCH, L. TOMIALOJC, P. J. WEISBERG, J. WOJNARSKI, R. A. FULLER, AND E. CANTARELLO. 2011. Global macroecology of bird assemblages in urbanized and semi-natural ecosystems. *Global Ecology and Biogeography* 20:426–436.
- PRODON, R., AND J. LEBRETON. 1981. Breeding avifauna of a Mediterranean succession: the holm oak and cork oak series in the eastern Pyrenees, 1. Analysis and modeling of the structure gradient. *Oikos* 37:21–38.
- RAJALA, M., O. RATTI, AND J. SUHONEN. 2003. Age differences in the response of willow tits (*Parus montanus*) to conspecific alarm calls. *Ethology* 109:501–509.
- SCHAEFFEL, F., AND H. WAGNER. 1996. Emmetropization and optical development of the eye of the barn owl (*Tyto alba*). *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 178:491–498.
- SHERRY, T. W., AND R. T. HOLMES. 1989. Age-specific social-dominance affects habitat use by breeding American redstarts (*Setophaga ruticilla*): a removal experiment. *Behavioral Ecology and Sociobiology* 25:327–333.
- SOL, D., D. M. SANTOS, AND M. CUADRADO. 2000. Age-related feeding site selection in urban pigeons (*Columba livia*): experimental evidence of the competition hypothesis. *Canadian Journal of Zoology* 78:144–149.

- VANDERHOFF, E. N., AND P. K. EASON. 2008. Comparisons between juvenile and adult American robins foraging for mulberry fruit. *Wilson Journal of Ornithology* 120:209–213.
- WAGNER, S. J., AND S. A. GAUTHREAUX, JR. 1990. Correlates of dominance in intraspecific and interspecific interactions of song sparrows and white-throated sparrows. *Animal Behaviour* 39:522–527.
- WEATHERS, W. W., AND K. A. SULLIVAN. 1991. Foraging efficiency of parent juncos and their young. *Condor* 93:346–353.
- WHITTAKER, K. A., AND J. M. MARZLUFF. 2009. Species-specific survival and relative habitat use in an urban landscape during the postfledging period. *Auk* 126:288–299.
- WOLF, B. O. 1997. Black phoebe (*Sayornis nigricans*). *Birds of North America* 268:1–20.

Submitted 26 September 2011. Accepted 1 September 2012.
Associate Editor was Karen E. Francl.