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Research Article

Evidence for frequency-dependent selection in House Wrens, but not Eastern Bluebirds

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Abstract. Frequency-dependent selection occurs when predators alter their prey choice to target abundant prey. We tested whether two species of insectivorous songbirds exhibited similar frequency-dependent selection behavior. House Wren (*Troglodytes aedon*) and Eastern Bluebird (*Sialia sialis*) routinely occupy nest boxes established over 700 acres at Missouri Western State University. During the 2018 breeding season from April through July, House Wrens consumed more sentinel prey from the color station that had previously appeared in higher frequency after four days of training. Eastern Bluebirds did not consume more of the previously abundant prey color stations and neither species showed a preference when the abundant color was reversed for the second half of the experiment which may be explained by latency in switching previously learned behaviors. Consequently, House Wrens demonstrated an initial frequency-dependent foraging strategy, but the Eastern Bluebirds did not. These results indicate how generalist insectivores that nest in the same habitat differ in their foraging strategies and behaviors.

Introduction

Predators learn from the environment and can form a search image based on a common prey morph they encounter leading to frequency-dependent selection (Clarke 1962). Frequency-dependent selection occurs when the predators shift this search image to the prey that is more common (Fitzpatrick et al. 2009). Tinbergen (1960) proposed the concept of the search image and framed the hypothesis that a predator would only discover and consume the prey after obtaining its search image. Frequency-dependent selection is an important aspect of foraging theory due to the potential to influence the rate of prey speciation (Melián et al. 2010) and maintain polymorphism in a population (Greenwood 1984; Fitzpatrick et al. 2009; Marples and Mappes 2011). Apostatic selection, preferring the common prey morph, promotes genetic and species diversity whereas anti-apostatic selection, preferring the rare prey morph, promotes uniformity (Church et al. 1997).

The frequency-dependent hypothesis comes with the assumption that reinforcement strengthens and shapes responses (Machado 1992), which requires intelligence. Among the animal kingdom, bird brain sizes are considered large relative to body size with some birds being well above average (Ricklefs 2004) thus arguing for high cognitive abilities. To partake in frequency-dependent selection, birds need to have mental time travel meaning they use past experiences to plan (Schacter et al. 2008). Birds also need what-where-when memory (WWW; Gallistel 1990; Feeney et al. 2011) which is

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important for developing a search image because the bird needs memory of what it is searching for and where it last found the prey item so that it can incorporate this information into its current food search. Studies that analyze frequency-dependent behavior also have to account for neophobia, which is an apparent hesitation when presented with novel prey (Brigham and Sibley 1999).

Frequency-dependent selection and foraging behavior are staples of the field of animal behavior and studies like Fitzpatrick et al. (2009) have focused primarily on prey responses in which there are different prey morphs based on predator preference. They found that the prey that was most common had a lower survival rate compared to the rare morph thus resulting in a maintained polymorphism in the salamander prey. Fifty years ago, Murton (1971) turned the focus on the predator, using Wood Pigeon (*Columba palumbus*) in frequency selection research. He found that pigeons consuming the largest quantity of prey were always the ones specialized on a certain prey type, and not those who were opportunistically foraging on whatever food they encountered. More recently, Bond and Kamil (2006) focused further on predator frequency-dependent selection with an emphasis on the role of prey backgrounds. They concluded that the polymorphism of cryptic prey is dependent not only on the habitat (background), but also predator cognition.

In this study, we researched whether bird species demonstrate a preference for a common prey item and if they are able to switch this preference. The two target species were native, cavity-nesting songbirds, House Wren (HOWR, *Troglodytes aedon*) and Eastern Bluebird (EABL, *Sialia sialis*), that breed in North America from April to August and have altricial young that require provision of food resources (Ligon and Hill 2010). Both species are generalist insectivores but have distinct foraging strategies; EABL primarily searches for prey visually from a perch and then drops to the ground to consume arthropods (Pinkowski 1977) whereas HOWR primarily gleans insects from leaf surfaces (Johnson 2014). We tested the presence of frequency-dependent selection in these birds using sentinel prey stations. Sentinel prey studies involve immobilized, tethered, or frozen prey to analyze predation (Jedlicka et al., 2011). We investigated that when these insectivorous birds were presented with equal distributions of the red or green sentinel prey stations, they would select prey from the color that was previously in higher abundance in accordance with the frequency-dependent hypothesis.

Materials and Methods

Study area

We conducted the study from early May through late June of 2018 on the 700-acre Missouri Western State University (MWSU) campus (39.7599° N, 94.7845° W), Saint Joseph, Missouri. The campus has a central core of university buildings surrounded by woodlands, hay fields, and riparian vegetation along the Otoe Creek that runs through campus. In 2016, 62 songbird nest boxes with a 3.81 cm diameter entrance hole were established in pairs across MWSU's campus and given unique identification numbers. The nest boxes were approximately 1.7 m from the ground erected on t-posts equipped with PVC predator guards located on the edge of woody vegetation facing East or North. The terrain in front of the nest boxes include both hay fields and grass lots that were mowed about once a month. Nest boxes were checked every three to four days to monitor nest activity, identify species, and record reproductive success. No birds were harmed in the duration of this experiment and research was carried out in accordance to IACUC permit #2016JED.01.

Sentinel prey experiment

A day after observing HOWR or EABL nestlings in a nest box, a background color (red or green) for the prey stations were randomly chosen to appear in higher frequency initially via a coin flip. Twenty-five cm^2 pieces were cut from cardboard and painted flag red or parakeet green (AppleBarrel Matte Acrylic Paint). Ten

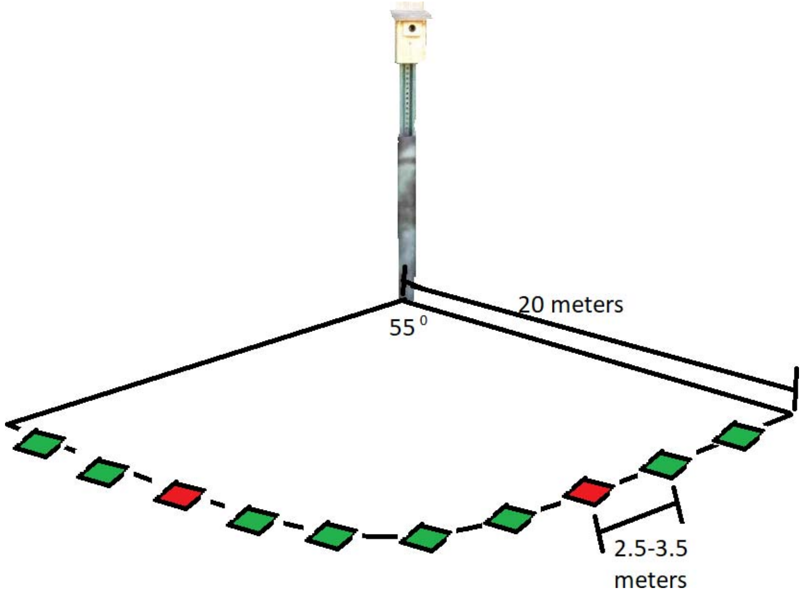

Figure 1. Experimental design of sentinel pest placement at nest box. Square colors correspond to the distribution ratio.

cardboard squares (hereafter stations) were used at each nesting site and had one large (1.9 to 2.5 centimeters long) mealworm food reward pinned through their last abdominal segment, immobilizing but not killing the insect (Jedlicka et al. 2011). The mealworms were pinned beginning at 04:30 and completed by 07:45. U-shaped garden stakes were used to secure the cardboard on the ground 20 meters in front of the nest box, in a 55 degree radius from the entrance hole, ~3 meters apart from one another (Fig. 1). The squares, stakes, and remaining mealworms were retrieved from each site at 13:00 the same day. The birds were not familiarized with the prey or colored backgrounds before running the experiment. Each experiment was conducted for 10 days at each box and as many as eight experimental sites were run simultaneously.

On day 1, 8 squares of the higher frequency color and 2 squares of the lower frequency color were put out. The frequency of colored stations changed over time similar to Fitzpatrick et al. (2009), where days 1-4 were training days of the 8:2 ratio and were followed with one test day (day 5) in which the prey were presented in a 5:5 ratio. Days 6-9 were also training days in which the opposite color was in higher frequency (2:8) to determine if the birds would switch their learned search image (Fig. 2; Allen et al. 1998). Day 10 was the final test day (5 of each color). A control site was used for each experimental site when feasible, where the sentinel prey were placed around a randomly chosen unoccupied nest box that had been occupied by that bird species the previous year. Data were collected on temperature, time of station implementation and retrieval, number of prey remaining per color, and color ratios.

Data analysis

The mealworms were considered consumed if they were completely missing or if they had been obviously mutilated (missing a head or most of their body). Mealworms that appeared to die from sun exposure were counted as present. Whole mealworms lying next to the cardboard square were scored as present due to the tendency to break after sun exposure. We also counted consumption of the mealworm by insects as present (for example, ants on the mealworm). In other words, mealworms were only counted as consumed if they were nowhere on or around the painted background. For test days, the number of

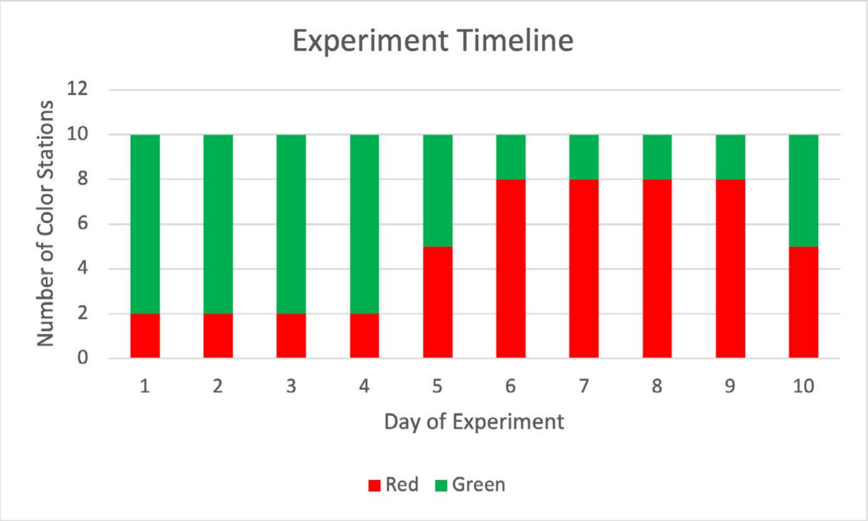

Figure 2. The progression of the high frequency and low frequency occurrences of the color stations during the experiment where green was selected to appear in high frequency first.

mealworms consumed on each color were tallied and we predicted that the color that was previously more abundant would be preferred. Because red and green stations were present in equal numbers (5 each) on test days, the probability of choosing any one color station on any one trial was 0.5. We used one-tailed sign tests (Dixon and Mood 1946) on SPSS ($\alpha = 0.05$) to examine whether there was any color preference by each bird species on test days (days 5 and 10). To control for neophobia, we also tested whether bird species consumed more sentinel prey as the experiment continued from day 1 through day 10 using a linear regression.

Results

In the course of the experiment, HOWR made 5 nesting attempts and EABL made 6 nesting attempts (with 1 suffering predation halfway through the experiment) in the 62 available nest boxes. Five HOWR and 5 EABL nesting sites were used for the experimental sites. HOWR demonstrated frequency-dependent selection by consuming significantly more prey from the previously high-frequency colored stations compared to the low-frequency stations on the first test day ($n = 5$; $p = 0.03$; Fig. 2), however, this trend did not reverse for the second test day ($n = 5$; $p = 0.25$). Unlike HOWR, EABL did not demonstrate frequency-dependent selection strategy for either test day ($n = 5$; $p = 0.25$ for both days 5 and 10). Of the 222 prey consumed by the HOWR, 49.1% were from red stations and 50.9% were from green. The same was true for the EABL; of the 168 prey consumed, 48.8% were from red stations and 51.2% were from green, indicating no inherent color preference. There were no changes in mealworm consumption throughout the experiment for both EABL ($R^2 = 0.007$, $p = 0.57$) and HOWR ($R = 0.006$, $p = 0.59$). Predation at the control sites was highly variable with no differences among the prey removed during test days ($n = 8$; $p = 0.58$ and $p = 1.0$ on first and second test day respectively). The control sites consumed an average of 2.5 (SE = 0.5303) prey from red stations and 2.25 (SE = 0.606) prey from green stations on the first test day. On the second test day, there was an average of 1.92 (SE = 0.6788) prey consumed from red stations and an average of 1.763 (SE = 0.6233) prey consumed from green stations.

Discussion

Our results showed frequency-dependent selection for HOWR nesting sites, but not

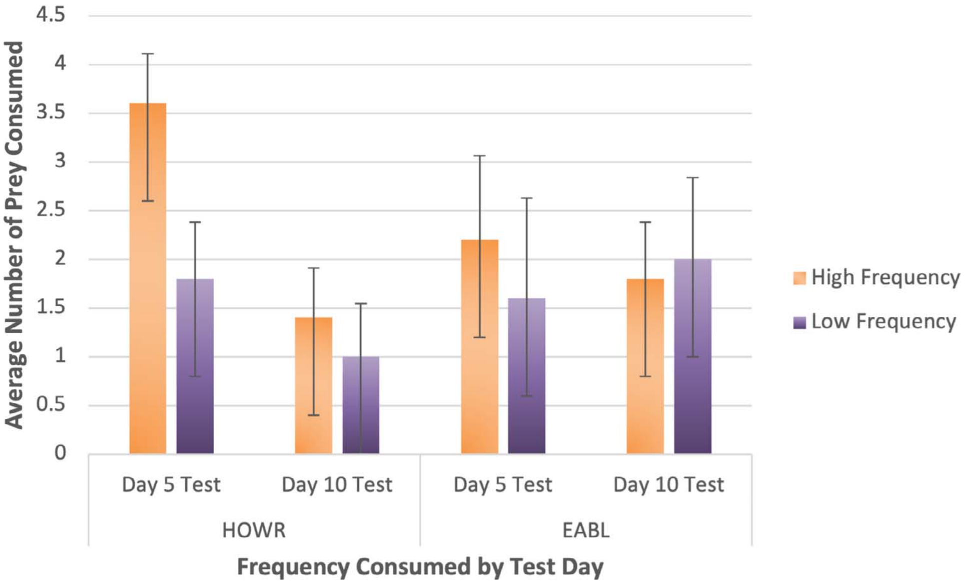

Figure 3. Average number (± SE) of sentinel prey consumed out of 5 total prey items at prey color stations that were previously high or low frequency during the earlier 4-day training period. Stations were placed below active House Wren (HOWR) and Eastern Bluebird (EABL) nest boxes.

EABL nesting sites and only during the first test day. This suggests that HOWR preferred the more common color stations initially but did not switch their preference in the following five days.

In order to ensure all sentinel prey items were visible and equidistant from the nest box we were limited to only 10 prey stations per box. Other studies (e.g. Weale et al. 2000) used higher abundances of prey organized into 'populations' within plots (e.g. 20 prey per m^2) to portray a density factor. While increasing the number of stations would increase statistical power, it would address different research questions that may be appropriate for future research. Other studies used prey that differed only in striping (Weale et al. 2000; Fitzpatrick et al. 2009), however some argue that this makes the prey too similar and birds may not exhibit a preference (Raymond and Allen 1990; Weale et al. 2000). Colors most commonly used in frequency-dependent studies are brown and green prey (e.g. Horsley et al. 1979; Allen et al. 1998; Weale et al. 2000) and there is some evidence that the birds' have an innate preference for brown prey (Allen 1998). To incorporate this potential bias, we chose to use the same prey species on different colored backgrounds (red or green), easily distinguished from the excellent color vision birds possess (Gill et al. 2019). The red and green stations were sufficiently dissimilar and thus theoretically allowed the birds to develop a non-innate preference. While these bird species regularly forage for prey against a green vegetative layer, neither HOWR nor EABL demonstrated a significant preference of the green background, so innate color preferences do not explain the differential results. It would be interesting, however, to use prey types that differed in color (similar to the differing backgrounds) to analyze whether that altered the frequency-dependent selection.

EABL and HOWR are generalist insectivores and consume a variety of insects during the breeding season (Johnson 2014) so why may HOWR adopt a frequency-dependent foraging strategy that was not present with EABL? EABL tends to utilize more perching foraging behavior than HOWR which utilize more gleaning behavior (Pinkowski 1977; Johnson 2014), so perhaps these differences in foraging strategies may favor different prey search patterns and alter the potential cost/benefit of frequency-dependent selection. For example, EABL may be able to search a larger area from a perch whereas the HOWR might be restricted to a smaller perceptual field during gleaning and thus be more reliant on prey images. Foraging behavior differences may emerge at low prey densities such that frequency-dependent selection might disappear and predators may adopt an opportunistic foraging strategy, consuming whatever they encounter (Allen et al. 1998). Measuring the abundance of environmental prey densities was outside the purview of this research, however, HOWR and EABL likely had access to similar arthropod quantities and so arthropod abundance does not explain the different behavior between the bird species. The two species also differ in their body and clutch size where EABL adults weigh 28–32 g with 2–7 eggs/clutch (Gowaty and Plissner 2015) and HOWR adults weigh 10–12 g with 2–10 eggs/clutch (Johnson 2014). Consequently, food requirements to support the energetic breeding costs may differ with these natural history tradeoffs albeit with unclear implications for potential foraging strategies between the species.

During the duration of the study, 11 of the 14 days with no predation were at EABL nest boxes so it could be possible that the birds interpreted the prey as novel and exhibited neophobia (Brigham and Sibley 1999; Marples and Mappes 2011). However, this did not seem to be an important variable in the study as both species did not consume more sentinel prey over the course of the experiment. It is also important to note that this experiment utilized a small sample size at one university campus and this should be taken into account to avoid overgeneralizations. Neither of the bird species in our study switched their prey preference during the second half of the study. In fact, with a similar experimental design to our study, Horsley et al. (1979) discovered that in the second half of the experiment birds seemed to select the rare prey form more strongly after experiencing the form when it was common. Guilford and Dawkins (1987) argue that previous evidence for the search image is not sufficient and instead the predators slow their search rate to find the ‘rare’ or ‘less obvious’ prey morph and that predators ‘learn to see’ the less obvious prey morph by this mechanism (Guilford and Dawkins 1987). Consequently, these data may support the search rate hypothesis because the birds did not ‘switch’ their preference every time. They argue that it could be the case that these bird species will never switch and continuously prefer the familiar prey, or it could be that the previously rare form was not given considerable time to become the ‘common’ form for the now experienced birds. Allen (1988) discusses that the search image helps explain frequency-dependent selection regarding polymorphic prey whereas slowing down the search rate does not. Further research is needed to distinguish between evidence for the search image hypothesis or the search rate hypothesis.

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