ABSTRACT: Little is known about cues used by insectivorous bark-foraging birds to locate prey. Because vision is thought to be the primary sensory system used by many avifauna to perceive the environment, we conducted an experiment to assess if insectivorous bark-foragers in northern Arizona forests used holes in trees as foraging cues. We set up 20 experimental stations, each consisting of a pair of equally sized ponderosa pines (Pinus ponderosa) that had no previous holes created by foraging woodpeckers or emergent boring-beetles. For each pair of trees, we drilled holes into one of the trees (treatment tree) and did not drill holes into the other (control tree). We monitored trees using trail cameras and reviewed photographs to determine: 1) at each station, was the first landing by each bark-foraging species on a treatment or control tree; and 2) how much time did bark-foragers spend on treatment vs. control trees? The experiment supported our hypothesis that bark-foragers used holes in trees as foraging cues. Twelve of 16 first-landing events were on treatment trees ($\chi^2 = 4.0, p < 0.05$), and 28 of 43 total photographs of bark-foragers were on treatment trees ($\chi^2 = 3.9, p < 0.05$). This experimental assessment of a visual foraging cue used by bark-foraging birds in the wild suggested that this guild may use holes created by woodpeckers or boring-beetles and larvae as a foraging cue.

Avian foraging ecology is important because birds may act as top-down ecosystem controllers, potentially having large impacts on prey communities and their functional processes (Wooten 1995; Rogers et al. 2013). Foraging cues are typically not included in avian foraging ecology studies, possibly due to the difficulties of creating controlled experiments in natural settings. Because cryptic prey are only available to a bird if the bird is capable of detecting the presence of that prey, understanding the foraging cues birds use to detect prey in any given habitat is fundamental to understanding their foraging ecology. Acquiring an understanding of avian foraging cues may be especially important for insectivorous bark-foragers such as nuthatches, creepers, and many woodpeckers that seek prey hidden under bark or wood because they can contribute to the control of forest tree pests to some extent (Kenis et al. 2004; Flower et al. 2014). Additionally, their populations have been demonstrated to be closely tied to forest disturbance and concomitant forest pest outbreaks (Crawford and Jennings 1989; Drever et al. 2008). As a result, avian bark-forager populations are sometimes considered as indicator species in forest management plans to assess the impacts of various forestry practices to their populations (Schick and Kenfield 2009; Euler 2014; Flower et al. 2014; Roberts and Burnett 2017).

A large body of literature, primarily based on aviary studies of a limited number of taxa, has documented innate and learned mechanisms of perceiving food (Tinbergen 1969; Adams-Hunt and Jacobs 2007). We know birds can use multiple sensory systems to locate food, such as audition (Floyd and Woodland 1981; Montgomerie and Weatherhead 1997), touch (Cunningham et al. 2009, 2010), vision (Adams-Hunt and Jacobs 2007; Rubene et al. 2019), and various forms of chemical perception (Saavedra and Amo 2018; Rubene et al. 2019). However, vision is thought to be the primary sensory system used by many bird species to perceive the environment (Zeigler et al. 1993; Jones et al. 2007). Even in those species that use other sensory systems to perceive food, vision may still play a partial role in food perception (Yang et al. 2015; Rubene et al. 2019).

Speculation in the literature suggests that bark-foragers use visual cues to find foraging trees, but a paucity of research informs the subject (Hammond and Theimer 2020). For example, because woodpecker foraging is often associated with decaying trees, Flower et al. (2014) suggested that the red-colored needles of dying softwood trees could potentially act as cues to foraging birds. To our knowledge, the only studies investigating foraging cues used by insectivorous bark-foraging birds documented that Pileated Woodpeckers (Dryocopus pileatus) are able to detect differences in ultraviolet wavelengths associated with food in a laboratory experiment (O’Daniels et al. 2017, 2018). This suggests that at least one insectivorous bark-foraging species may use visual cues to locate prey. In June 2018, we documented a bark-foraging species, the Hairy Woodpecker (Dryobates villosus), landing on trees and immediately climbing up and down the trunk while peering into existing holes created by woodpeckers to excavate food (RLH
unpubl. data), Lawrence (1967) made similar observations, and at least 2 other studies suggested that bark-foragers may be attracted to nest-hole or food excavation sites of woodpeckers (Kilham 1970; Saenz et al. 2002). Taken together, these observations suggest that holes may act as cues to bark-foragers.

We conducted an experiment to test 2 predictions of the general hypothesis that bark-foragers use holes in the bark as foraging cues: 1) birds should land on a tree with artificially created holes before landing on a nearby tree without holes; and 2) birds should use trees with artificially created holes more often than a nearby tree without holes. To our knowledge, our study is the first to experimentally assess visual foraging cues of bark-foragers in the wild. Although avairy studies are invaluable to understanding avian foraging, they fail to include natural factors that may affect food perception or foraging decisions in nature, such as the presence of predators, auditory and visual obstructions, and physiological constraints (Ydenberg et al. 2007).

METHODS

Study Site and Species

We conducted our experiment in the Coconino National Forest surrounding Flagstaff, Arizona between March and November 2019 (Figure 1). Our sites were dominated by ponderosa pine with scattered Gambel oaks (Quercus gambelli) and/or one-seed juniper (Juniperus monosperma). Our study focused on 6 bark-foraging species, including Hairy Woodpecker, Red-naped Sapsucker (Sphyrapicus nuchalis), Williamson's Sapsucker (Sphyrapicus thraoides), Pygmy Nuthatch (Sitta pygmaea), White-breasted Nuthatch (Sitta carolinensis), and Brown Creeper (Certhia americana). Although woodpeckers are likely the only species that create foraging holes in trees, we included other bark-foragers because the bark-foraging guild often forages in mixed-species flocks (Stallcup 1968; Dolby and Grubb 1988; Waite and Grubb 1988); foraging behavior is learned from other species in mixed-species flocks (Giraldeau 1984; Slagsvold and Weibe 2011); and individuals may be more likely to follow heterospecifics than conspecifics when foraging in mixed-species flocks, possibly to avoid agonistic interactions with conspecifics (Waite and Grubb 1988). Further, holes in trees occur for reasons other than woodpecker excavation (e.g., emergence and oviposition holes of bark- and wood-boring insects), and, like bark crevices, serve as shelter sites for insects and their eggs, suggesting that holes have the potential to be useful foraging cues for nonwoodpecker bark-foragers. Although sapsuckers are named for their specialized diet on tree sap, we included them in our study because they do forage in mixed flocks (Morse 1970; Gram 1998; Schaefer et al. 2004; Farley et al. 2008) and include insects as part of their diets (Bent 1939; Stallcup 1968; Bull et al. 1986), sometimes making up nearly 50% of stomach contents (Beal 1911). We did not include other common local woodpeckers, such as Northern Flicker (Colaptes auratus) and Acorn Woodpecker (Melanerpes formicivorus), in our study because bark-dwelling insects are uncommon in their diets (Beal 1911).
Experimental Design

At each of 20 experimental stations, we located 2 ponderosa pines that had diameters at breast height (dbh) of ≥35cm. It is rare for live ponderosa pines smaller than this to have woodpecker excavation holes and/or wood-borer emergence holes in our study area (RLH unpubl. data). Because woodpeckers often prefer larger trees for foraging (Hammond and Theimer 2020), each pair of trees was chosen to have no more than a 5 cm difference in dbh to prevent any confounding effects of tree size. We also ensured that both trees had no previously existing holes created by birds or insects, and that both appeared healthy (i.e., trees had green needles, no broken tops, and no large cracks in the trunk or missing sections of bark). One of the trees was randomly assigned as a control tree (i.e., we did not drill holes into it), and the other as a treatment tree (i.e., we drilled holes into the tree). In order to accurately mimic the natural pattern of woodpecker and wood-borer holes in live trees, we selected a tree from our sample of 120 trees, assessed as part of a larger woodpecker foraging ecology study that had an average number of holes (58) within a 1-m2 section of the trunk centered at breast height (1.3m) (Figure 2). We used that tree as a template and used a transparent painter’s tarp to mark the 58 holes, so that the holes in the template could be overlaid and drilled at the same place on treatment trees. We drilled holes into treatment trees using a 17/64-inch drill bit to a depth of 1.5 mm to avoid resin exudation, which could have confounded the study if birds use chemical cues.

At each of the 20 stations, we attached 2-4 trail cameras (Wingscapes Birdcam, model WSCA01) to trees at 4-8 m from each experimental and control tree so that photographs were taken at 2 sides of each tree, in an attempt to detect birds landing anywhere we drilled holes. Because the trail cameras would not reliably trigger by motion at the distance we placed them, we used the time-lapse feature to take one photograph per minute during the daylight hours for 6 weeks. In order to attract birds to the vicinity of each station, we hung a suet cage between 5-20 m from experimental trees at a location that was approximately equidistant from the control and treatment trees.

Data Analysis

We reviewed photographs from all cameras twice to identify bark-foragers that landed on the lower trunk of study trees (Figure 3). We attempted to identify all birds to species, but when identification to species was not possible, we tried to determine if the bird was a woodpecker (categorized as unknown woodpecker) or nuthatch (categorized as unknown nuthatch). In some cases, we could not place the bird into any group and the species was categorized as unknown. We noted for each landing whether the bird was first recorded on a control or treatment tree and recorded how many consecutive photographs the bird remained in view on the tree.
We tested our first prediction by assessing at each station whether the first photograph of a bird on a tree occurred on a control or treatment tree for each bird species. Because we had small sample sizes, we could not conduct an analysis by species, so we pooled data on first landing events and used a chi-squared test to determine if there was a significant difference between the number of first-landings on control vs. treatment trees. For this analysis, we did not use photographs of birds when we could not identify the bird in the photograph to species if there were any other photographs of identifiable birds at the station. We did not use those photographs because the unidentifiable individual could have been a bird belonging to a species that had already been detected at the station (i.e., if an unknown bark-forager landed on a tree at one time and any other species was positively identified at any other time during monitoring, we excluded the photograph of the unidentifiable bird). To address our second hypothesis, we used a chi-squared test to assess whether there was a significant difference between total number of landings by all bark-foragers on control vs. treatment trees for the duration of the study. Because we did not need to differentiate between first-landing events by species in the second analysis, the fact that we could not identify all individuals to species was not important, so we included all photographs.

Figure 3. Sample photographs of bark-foraging birds captured on experimental trees: a) female Hairy Woodpecker on treatment tree; b) male Williamson’s Sapsucker on control tree; c) unknown woodpecker on treatment tree; d) White-breasted Nuthatch on treatment tree at study sites in the Coconino National Forest near Flagstaff, Arizona.
RESULTS

Ten of the 20 experimental stations were visited by one or more bark-foraging birds, including Red-naped and Williamson's Sapsuckers, Hairy Woodpecker, White-breasted Nuthatch, and Brown Creeper (Table 1). Our first prediction was supported, with 12 of 16 first-landing events on treatment trees ($\chi^2 = 4.0, p < 0.05$). Our second prediction was also supported, with 28 of 43 photographs of bark-foragers on treatment trees ($\chi^2 = 3.9, p < 0.05$).

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<th># Total Pictures</th>
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DISCUSSION

When we pooled observations across all bark-foraging species, both of our predictions were supported, suggesting that at least some bark-foragers may use holes in trees as foraging cues. We documented few landing events for Brown Creepers and both sapsuckers, making it impossible to draw any inferences about use patterns in those species. Pygmy Nuthatches were common in our study area and we expected them to land on study trees, but their tendency to spend more time foraging on twigs than on trunks may have led to the lack of positively identified photos of this species relative to White-breasted Nuthatches, which primarily forage on trunks (Stallcup 1968).

Of the 2 species that were the most documented at our stations, Hairy Woodpeckers and White-breasted Nuthatches both tended to land on treatment trees first, but the total number of times each was recorded on experimental and treatment trees differed. Eighty-eight percent of photographs of Hairy Woodpeckers were on treatment trees, while 38% of White-breasted Nuthatch photographs were on treatment trees. The fact that White-breasted Nuthatch first-landing events were greater on treatment trees than control trees, but number of landing events were not very different between tree type, may not necessarily suggest that White-breasted Nuthatches did not use holes as a foraging cue, but instead that number of landings was a less-accurate assessment of foraging cue use compared to first-landings. First-landings indicate the initial choice a bird makes about where to land to forage, so it reflects selection at the tree level. Our results indicated that the presence of holes affected that choice in both Hairy Woodpeckers and White-breasted Nuthatches. After the bird was initially attracted to the tree, use of the tree thereafter may be more likely governed by food availability. For example, it may be that after White-breasted Nuthatches had selected the treatment tree based on our false cue, they then abandoned the tree because prey densities were below the level of that expected in the habitat (i.e., below the “giving up density”; Brown 1988). Likewise, most of the photographs we captured of White-breasted Nuthatches on control trees were on only 2 of the 20 control trees at our experimental stations. If those 2 control trees had higher than average prey densities, nuthatches may have stayed longer on those trees, independent of any foraging cue.
Our study was the first to experimentally demonstrate the use of a visual foraging cue in wild bark-foraging birds, but was limited by small sample sizes, which may have occurred due to seasonal constraints. Half of our stations were never visited by bark-foragers. Lack of visitation by bark-foraging birds to those trees may have occurred, in part, because we set up 14 of the 20 experimental stations in summer. Of the 43 photographs we obtained of bark-foragers, only 6 were taken during summer months, suggesting that the foraging cue may have been more important to birds during cold months. This conclusion makes sense when we consider the seasonal foraging behavior of Hairy Woodpeckers, which excavate for food more in cold vs. warm months, presumably due to the low insect densities on bark surfaces during cold months; thus making foraging cues for subsurface prey more important in cold months (Conner 1981). Only one White-breasted Nuthatch photograph was taken during the summer, suggesting that this species was also more responsive to the cue during cold months, even though it does not excavate for prey. The suet, which we used to attract birds to experimental stations, appeared to have been more important to birds during cold months, when insect prey densities are typically low in temperate regions, and food is more difficult to locate. Although we did not collect data to rigorously monitor the suet depletion rate, suet was used little in summer months, with only a few of stations needing to have the suet replaced during the 6-week sampling period. In contrast, during cold months suet needed to be replaced at least 3 times during the sampling period, suggesting that birds were using the stations more, and that birds were, thus, more likely to interact with our experimental and control trees.

Although our study suggested that holes in the bark may be important cues for selecting foraging trees by bark-foraging birds, other cues should be investigated. For example, researchers could assess if indicators of tree weakness relate to tree pest presence (Flower et al. 2014). Authors might also investigate how cues related to other sensory systems could be used by birds to detect prey. Olfaction is an important cue used by other avian taxa for locating insects (Amo et al. 2013; Saavedra and Amo 2018; Rubene et al. 2019). Given that tree chemical properties may attract or repel bark- and wood-boring insects (Byers 1995), and that pheromones are used by bark- and wood-boring insects to attract or repel other insects (Raffa 2001; Raffa et al. 2015), bark-foraging birds may also be able to use these chemical cues to locate prey. The use of taction, or “percussive foraging”, has been documented in a mammalian primate known as the Aye-Aye (Daubentonia madagascariensis) when searching for subsurface insect larval prey (Erickson 1994). Because bark-foraging birds will similarly excavate and/or flake bark from trees to access prey, the use of taction to detect subsurface prey movement may also serve as a cue in the bark-foraging bird guild.

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LITERATURE CITED


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