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Functional significance of ultraviolet feeding cues in wild turkeys

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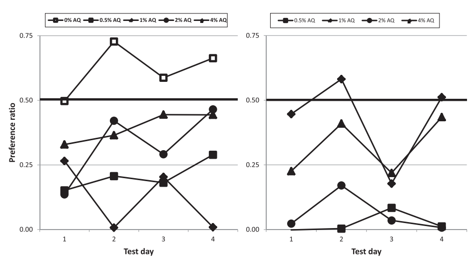
HIGHLIGHTS

- Wild turkeys do not prefer UV feeding cues regardless of feeding experience.
- UV feeding cues are used functionally for avian foraging behavior.
- Postingestive consequences are necessary for conditioned avoidance of UV feeding cues.
- Intestinal parasite infection influences the process of food selection in wild turkeys.

GRAPHICAL ABSTRACT



Preference ratios for female wild turkeys offered untreated food and food treated with an UV-absorbent cue during a 4-day preference test. Preference ratios >0.5 indicate preference for treated food; ratios <0.5 indicate avoidance of treated food. The control group (unfilled squares) was exposed to unadulterated oats and test groups (filled shapes) were exposed to 0.5%, 1%, 2%, or 4% anthraquinone prior to the test of conditioned avoidance.

Preference ratios for male wild turkeys offered untreated food and food treated with an UV-absorbent cue during a 4-day preference test. Preference ratios >0.5 indicate preference for treated food; ratios <0.5 indicate avoidance of treated food. Test groups were exposed to 0.5%, 1%, 2%, or 4% anthraquinone prior to the test of conditioned avoidance.

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ABSTRACT

Most birds are able to sense ultraviolet (UV) visual signals. Ultraviolet wavelengths are used for plumage signaling and sexual selection among birds. The aim of our study was to determine if UV cues are also used for the process of food selection in wild turkeys (*Meleagris gallopavo*). We used avoidance conditioning to test the hypothesis that UV feeding cues can be used functionally for foraging behavior in wild turkeys. Female turkeys exhibited no avoidance of untreated food and 75–98% avoidance of food treated with an UV-absorbent, postingestive repellent (0.5–4% anthraquinone; wt./wt.) during repellent exposure. Male turkeys exhibited 78–99% avoidance of food treated with 0.5–4% anthraquinone. Female and male turkeys that consumed more than 200 mg and 100 mg of anthraquinone, respectively, subsequently avoided food treated only with an UV-absorbent cue. In contrast, unconditioned females consumed 58% more food treated with the UV-absorbent cue than untreated food. Thus, wild turkeys do not prefer foods associated with UV wavelengths regardless of feeding experience. We also observed 1) a weak negative correlation between body condition and intestinal parasite infection and 2) moderate, positive correlations between consumption of food treated with the conditioned UV cue and intestinal parasite infection among male turkeys. The UV feeding cue was used to maintain food avoidance during the four days subsequent to postingestive conditioning. Moreover, the consequences of consuming food treated with the postingestive, UV-absorbent repellent were necessary for conditioned avoidance of the UV-absorbent cue. These findings suggest functional significance of UV feeding cues for avian foraging behavior, the implications of which will enable subsequent investigations regarding the sensory physiology and behavioral ecology of wild birds.

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1. Introduction

Most birds appear to be capable of sensing UV visual signals [1], but little is known about how they functionally use this information,

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particularly in the context of foraging. Ultraviolet cues could be used for foraging in two ways: 1) to detect foraging patches and recognize individual food items, and 2) to assess the relative quality of food items [2]. Comparative studies have found that not all bird species that could benefit from the use of UV feeding cues have evolved the retinal color receptors to do so (e.g. plunge-diving seabirds; [3]). Intraspecific studies have demonstrated that some bird species do indeed use UV cues to detect their food. Diurnal, predatory birds such as the Eurasian kestrel (*Falco tinnunculus*), rough-legged buzzard (*Buteo lagopus*) [4] and the great grey shrike (*Lanius excubitor*; [5]) use the UV reflectance of rodent urine to choose foraging patches where they are more likely to find these prey. Similarly, blue tits (*Parus caeruleus*) are able to find the first of a set of experimentally hidden cabbage moth (*Mamestra brassicae*) caterpillars more quickly with UV illumination than without it [6].

Many of the fruits eaten by birds exhibit high UV contrast with their backgrounds [7,8]. In a field study where UV filters were placed over *Psychotria emetica*, a tropical understory shrub, fewer fruits were taken when UV irradiance onto fruits was blocked compared to when UV transmitting filters were used [9]. Of course birds are not the only taxa to rely upon UV cues to detect their food. Predatory jumping spiders (*Portia labiata*) are preferentially attracted to the webs of their prey spider (*Argiope versicolor*), but only when the web reflects UV wavelengths [10]. Thus, birds and other animals can detect food more easily using UV cues. It is not clear, however, if birds use UV cues to assess the quality of their food.

Although both the strength of UV reflectance and predator preferences are often positively associated with specific prey, it is not known if preferences associated with UV reflectance increase the lifetime fitness of the forager. Are UV-reflecting prey more nutritious (sensu lato)? For example, are the prey biases observed among kestrels, for male rodents and for certain rodent species (see review; [2]), simply due to differences in signal detectability (i.e. greater UV reflectance) or have these predators learned that prey that exhibit greater UV reflectance provide greater benefits (e.g. more fat resources or fewer parasites)? Unfortunately very little is known about how birds utilize UV feeding cues; are there innate preferences for UV-reflecting or UV-absorbing food, or do birds learn to associate UV cues with food quality?

Ecologically-relevant, newborn color preferences and ontogenetic changes in color preferences have been studied experimentally in birds using only human-perceived colors (400–700 nm). Because of their experimental tractability, most of these studies have used domestic fowl (*Gallus gallus domesticus*) chicks as study subjects. Newborn domestic chicks prefer food items that are red or green in color if they are fruit-shaped, but avoid red items that are insect-shaped [11]. Chicks learn more easily to avoid distasteful food items that are red or yellow [12], or that contrast with their background [13], but some combinations of color and palatability are difficult for them to learn. For example, chicks require exposure to high quinine concentrations in their prey to learn that purple is unpalatable, but low quinine levels are sufficient for them to learn to avoid distasteful green prey [13].

Ontogenetic differences have been observed in UV foraging preference in redwings (*Turdus iliacus*; [14]). They discovered that wild-caught adult redwings preferred UV-reflecting bilberry (*Vaccinium myrtillus*) fruits over bilberries whose UV-reflecting waxy coat had been removed, but only when UV illumination was provided. Naïve, captive-reared redwing juveniles, however, showed no preference for the UV-reflecting fruits in either lighting regime, suggesting that redwings must learn to prefer UV wavelengths (or that their UV perception develops later in life). Ripe fruits often reflect more UV wavelengths [9], possibly explaining why many birds are attracted positively to UV wavelengths. Alternatively, plants may have co-opted existing avian preferences for UV-reflecting mates through sensory exploitation [15] in order to achieve greater seed dispersal by avian frugivores. Others posit that UV wavelengths have no special “meaning” via sensory bias [16], but are simply another color for which birds must learn context dependency (just as birds must learn that some red fruits are unpalatable; [17]). To better understand how birds can use UV feeding cues, we experimentally investigated the foraging behavior of avian subjects with UV vision.

We used the wild turkey (*Meleagris gallopavo*) to investigate the functional significance of UV feeding cues. Wild turkeys are omnivores who consume a wide variety of vegetation, fruits, seeds, insects and other invertebrates [18]. Several lines of evidence support our contention that UV vision is important to turkey natural history. First, domestic turkeys (*M. gallopavo*) are attracted to housing with UV lighting [19]. Second, although they lack UV-sensitive opsin photopigments, ocular oil droplets associated with their short-wavelength sensitive cones apparently permit UV vision [20]. Domestic turkeys have considerable sensitivity to wavelengths in the UV-A spectral range (315–400 nm; [20]). Increment threshold psychophysiological tests have shown that domestic turkey poults are maximally sensitive to the UV spectrum at 380 nm [16]. Other studies have demonstrated that UV vision is probably of relevance to the social and sexual interactions of turkeys as well. The intensity of the UV reflectance of iridescent feathers from male wild turkeys is condition-dependent [21] and the plumage of domestic turkey poults exhibits UV-reflective patterning that is associated with body sites of harmful pecking in commercial poultry houses [22]. Moreover, another wild species in the order Galliformes, the black grouse (*Tetrao tetrix*), prefers UV-reflecting morphs of a fruit that is a seasonally important component of their diet [23].

Because the implications of UV cues are poorly understood for avian foraging behavior, we compared the feeding response of conditioned and unconditioned wild turkeys offered food treated with an UV-absorbent cue subsequent to conditioning with an UV-absorbent, postingestive repellent. If wild birds prefer foods associated with UV wavelengths regardless of feeding experience (hypothesis 1), then conditioned and unconditioned wild turkeys will prefer foods treated with an UV cue. If UV feeding cues, like other visual and gustatory cues [24,25], are used functionally for avian foraging behavior (hypothesis 2), then wild turkeys conditioned with an UV-absorbent, postingestive repellent will subsequently avoid food treated with an UV-absorbent cue, even in the absence of the aversive consequence.

Although intestinal parasite infection (e.g. *Eimeria* spp.) decreases food consumption in domestic turkeys [26–29], the effects of body condition and parasite load are poorly understood for the process of food selection. Coccidia infection influences sexual selection among female wild turkeys [30] and UV plumage signaling among male wild turkeys [21]. Body condition or parasite infection of wild turkeys may also influence an individual's selection of food treated with an UV cue previously paired with negative postingestive consequences. If body condition or parasite infection influences the process of avian food selection (hypothesis 3), then consumption of food treated with an aversively-conditioned UV cue will be least among wild turkeys with poor body condition or high parasite infection.

2. Feeding experiments

2.1. Subjects and testing facilities

Wild turkeys (4–6 years of age) were maintained at the Department of Biology's Avian Research Facility at the University of Mississippi Field Station in Lafayette County, Mississippi, USA. The wild turkey flock of game farm origin was raised in captivity from hatching. Twenty netted enclosures ($4.0 \times 3.7 \times 1.8$ m) were established within a 0.04-ha flight pen for the study of hens (i.e. female wild turkeys; body mass average = 4.07 kg, range = 3.02–5.75 kg). We used 16 individual cages ($2.4 \times 1.5 \times 1.8$ m) within an open-sided research aviary for the study of gobblers (male wild turkeys; body mass average = 9.87 kg, range = 7.45–11.50 kg). Clean water was provided ad libitum to all test subjects throughout the study.