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Use of visual and olfactory sensory cues by an apex predator in deciduous forests

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Abstract

Predator-prey interactions influence behaviors and life history evolution for both predator and prey species and also have implications for biodiversity conservation. A fundamental goal of ecology is to clarify mechanisms underlying predator-prey interactions and dynamics. To investigate the role of predator sensory mechanisms in predator-prey interactions, specifically in predator detection of prey, we experimentally evaluated importance of visual and olfactory cues for an apex predator, the coyote (*Canis latrans* (Say, 1823)). Unlike similar studies, we examined use of sensory cues in a field setting. We used trail cameras and four replicated treatments—visual only, olfactory only, visual and olfactory combined, and a control—to quantify coyote visitation rates in North American deciduous forests during fall 2016. Coyote visitation was greatest for olfactory- and visual-only cues, followed by the combined olfactory-visual cue; all cues attracted more coyotes than the control (i.e., olfactory = visual > olfactory-visual > control). Our results suggest this apex predator uses both olfactory and visual cues while foraging for prey. These findings from a field study of free-roaming coyotes increase understanding of predator foraging behavior, predator-prey interactions, and sensory ecology. Our study also suggests future directions for field evaluations of the role of different sensory mechanisms in predator foraging and prey concealment behaviors.

Keywords: *Canis latrans*, coyote, foraging ecology, habitat selection, habitat use, olfactory concealment, predator-prey interactions, sensory cues, visual concealment.

Introduction

Predator-prey interactions are a key class of community interactions that influence ecosystem dynamics (Dulvey et al. 2004; Beauchamp et al. 2006; Ripple and Beschta 2012), drive behavioral and life history evolution of predator and prey species (Berryman 1992; Abrams 2000), and have important implications for biodiversity conservation (Sinclair et al. 1998; Ritchie and Johnson 2009). The sensory mechanisms used by predators to detect and locate prey (e.g., visual, olfactory, aural, tactile, and thermal) are a fundamental aspect of predator-prey interactions that influence both predator foraging behavior (Santisteban et al. 2002) and prey morphological and behavioral traits (e.g., background matching and habitat selection, respectively) (Shivik and Clark 1997; Caro 2005; Merilaita and Lind 2005). Understanding the sensory mechanisms predators use to detect prey is therefore essential for elucidating short-term predator hunting and prey avoidance behaviors, as well as long-term life history evolution and evolutionary “arms races” between predator and prey species (Dawkins and Krebs 1979).

Predators use both direct cues, where prey are identified and located instantaneously (e.g., visual detection), and indirect cues, where detection precedes the actual location of prey (e.g., olfactory detection of prey scent or aural detection of prey sounds) (Carthey et al. 2011). Observational and experimental studies illustrate that most mammalian and snake predators rely primarily on olfaction (Burghardt 1966; Halpern and Frumin 1979; Roth et al. 1999) while avian predators hunt primarily using visual cues (Dwernychuk and Boag 1972; Sugden and Beyersbergen 1986; Nams 1997; Slotnick 2001). Although the majority of previous research into predator detection mechanisms has investigated the response of predators to a single sensory cue (but see Santisteban et al. 2002; Hughes et al. 2010), predators can use multiple sensory cues simultaneously and/or sequentially (Conover 2007). Furthermore, because the conspicuousness

of each sensory cue is differentially affected by environmental conditions, predators should benefit from such synergistic use of multiple detection mechanisms (Shivik and Clark 1997). Indeed, most mammalian predators are opportunistic hunters that vary their use of visual, olfactory and/or aural cues depending on the efficiency of each cue under particular environmental conditions and circumstances (Conover 2007). For example, wolves use olfactory cues for long-range prey tracking and visual cues to hone in on prey at short ranges (Mech 1970), and although snakes are predominantly olfactory predators, they regularly employ vision, and some taxa (e.g., vipers) use infrared radiation when environmental conditions are unfavorable for olfactory detection (Conover 2007).

Numerous factors influence the potency, longevity, and therefore, the detectability of sensory cues. For example, topography, vegetation structure, light levels, and weather (e.g., visibility and precipitation) influence the ability of predators to detect prey using visual cues (Redmond et al. 1982). Likewise, many weather conditions (e.g., relative humidity, precipitation, and wind velocity, turbulence, and updrafts) interact with vegetation and topography to influence the ability of predators to detect prey using olfactory cues. For example, high air turbulence intensity near ground level disperses and dilutes odor molecules and can decrease predator detection of prey items (Conover 2007; Fogarty et al. 2018), and low-moisture conditions reduce mobility and thus detectability of odor molecules relative to moist conditions (Vander Wall 1998, 2003). These factors lead to general patterns in predator foraging strategies, such as predominant use of visual foraging by diurnal predators due to favorable light levels during the day (Conover 2007) and predominant use of olfactory foraging by nocturnal and crepuscular predators due to high humidity levels that enhance olfactory detection during these time periods (Caro 2005).

To further expand our understanding of how sensory detection mechanisms influence predator-prey interactions—specifically, predator foraging and detection of prey—we conducted an experimental study using trail cameras to examine the relative importance of visual and olfactory mechanisms of prey detection for an apex predator, the coyote (*Canis latrans* (Say, 1823)), in eastern North American forests. Similar to other mammalian predators, coyotes can be active throughout the day and night when inhabiting environments not heavily disturbed by humans, and they can use both visual and olfactory cues to locate prey (Wells and Lehner 1978; Turkowski et al. 1983; McClennen et al. 2001). However, the relative importance of these sensory cues in a natural setting is unknown. Because past lab-based studies have indicated coyotes may preferentially use visual detection (Wells 1978; Wells and Lehner 1978; Baker et al. 2011), we hypothesized that coyote visitation would be greater at a visual-only cue compared to an olfactory-only cue. We also hypothesized that cameras with a combined olfactory-visual cue would be visited more frequently than either the visual- or olfactory-only treatments.

Materials and methods

Study System

The study area consisted of two sites in Oklahoma, USA, including Cookson State Wildlife Management Area (hereafter Cookson WMA) (35°40'08.2"N, 94°49'20.9"W) and the J.T. Nickel Family Nature and Wildlife Preserve (hereafter Nickel Preserve) (36°02'03.8"N, 94°48'29.7"W) (Fig. 1). These properties are respectively managed by the Oklahoma Department of Wildlife Conservation and The Nature Conservancy. Both sites are in the Cookson Hills of eastern Oklahoma, the westernmost extension of the Ozark Plateau. This region consists predominantly of oak-hickory forest interspersed with savanna, shrubland, and tallgrass prairie;

the forest vegetation is dominated by oak species (*Quercus rubra* (L.), *Q. velutina* (Lam.), and *Q. alba* (L.)), hickory species (*Carya* spp. (Nutt.)) and shortleaf pine (*Pinus echinata* (Mill.)) (Graney 1997; Guyette et al. 2006). Elevation within the sites ranged from 230 m to 380 m a.s.l. The Cookson Hills have a humid continental climate, with an average low temperature of -2.7 °C in winter, an average high temperature of 33.1 °C in summer, mean annual precipitation of 127.59 cm, and an average of 82 rainy days per year. The mammalian predator community consisted of coyote, northern raccoon (*Procyon lotor* (Linnaeus, 1758)), Virginia opossum (*Didelphis virginiana* (Kerr, 1792)), bobcat (*Lynx rufus* (Schreber, 1777)), nine-banded armadillo (*Dasypus novemcinctus* (Linnaeus, 1758)), feral pig (*Sus scrofa* (Linnaeus, 1758)), American black bear (*Ursus americanus* (Pallas, 1780)), and gray fox (*Urocyon cinereoargenteus* (Schreber, 1775)). Primary management activities include feral pig trapping and removal, prescribed fire, and on Cookson WMA, timber harvest, controlled hunts, and furbearer trapping. However, at Cookson WMA, furbearer trapping was relatively light during the years leading up to our study, and hunting and trapping were not ongoing during our research period (C. Allen, Oklahoma Department of Wildlife Conservation, *personal communication*). We therefore had no reason to expect that past trapping would lead to systematic biases in coyote visitation toward any of the experimental treatments described below.

Study Design and Data Collection

The study occurred during two sampling periods in 2016; the first period was from 24 September to 16 October at Cookson WMA, and the second was from 06 November to 03 December at Nickel Preserve. We used Google Earth (Google Inc., Mountain View, California) to generate three 900 m transects at each study site (6 transects total), with each transect

consisting of four points spaced 300 m apart. This distance of separation was selected to maximize independence of treatments while facilitating logistic ease of access for camera maintenance; however, as described below, we also accounted for potential spatial autocorrelation among points on the same transect by treating transects as a random effect. Because different vegetation communities harbor different predator communities, and also because predators are likely to use different sensory cues in different vegetation communities (Patten and Smith-Patten 2012; Fogarty et al. 2018), we sought to minimize variability in vegetation cover both within and among transects by locating all transects in continuous forest cover and parallel to roads, ridgelines, or drainages. Coyotes may travel across the landscape parallel to such linear features; however, our approach of randomizing treatments along transects (see below) should account for this and any other factors that might lead to certain points on transects being visited more frequently. To minimize spatial autocorrelation and to ensure we captured independent predator assemblages at each transect, all transects were located ≥ 2000 m from each other. To facilitate logistic ease of sampling, all transects were < 100 m from a road.

To evaluate predator detection and attraction to different sensory cues (hereafter cues), we randomly assigned one of four cue treatments (olfactory, visual, olfactory and visual, or control; see Figure 2 for an example of the olfactory and visual treatment, which includes components of both the visual- and olfactory-only treatments) to points along each transect, such that each transect included all four treatments. All sensory treatments were designed to represent cues emanating from an avian prey item because dietary assessments from the same region (Arkansas, USA) show that birds are among the most common prey item for coyotes (Gipson 1974). However, based on the assumption that coyotes use similar cues to forage for most common prey items, results from this experiment should be generalizable to other prey taxa. The

olfactory cue consisted of non-synthetic, concentrated Mourning Dove (*Zenaida macroura* (Linnaeus, 1758)) scent (National Scent Company, Memphis TN) placed in a scent drip (Wildlife Research Center, Ramsey, MN) elevated 0.5 m above ground-level with a small platform attached directly below the drip; this setup simulated an odor emanating from a bird 0.5 m above ground-level rather than from directly on the ground. Scent drips contained enough concentrated Mourning Dove scent to maintain a fresh olfactory cue for up to two weeks, with scent released periodically throughout the day. The visual cue consisted of a plastic, non-mechanical Mourning Dove decoy (Academy Sports and Outdoors, Katy, TX) with an anti-glare flocked finish that was perched on a wooden stake 0.5 m above ground-level; to simulate an injured wing, we affixed a painted cut-out wing made from 4-mm thick corrugated plastic. The combined visual and olfactory cue consisted of both the scent drip/platform and the dove decoy placed next to each other at 0.5 m above ground level. The control treatment included no sensory cues.

One remote sensing trail camera (Browning Range Ops Series, model BTC-1) was placed at each treatment replicate, such that the camera was mounted to a tree between 0.4 and 1.5 m above ground-level, and 1-2 m from and facing toward the treatment setup. Cameras were programmed to trigger with any motion detection and to have a 30-second timeout period between photo bursts to limit consecutive captures of the same individual and therefore save memory card space (Elizondo and Loss 2016). During each sampling period, all transects were visited once to replenish scent drips, check camera batteries, and repair any damage to the experimental treatment setups. Although we did not directly handle wild animals, our sampling protocol was approved by the Institutional Animal Care and Use Committee at Oklahoma State University (Protocol #AG-14-7).

Data Analysis

During analysis of camera trap images, we only considered images of coyotes to be unique individuals if the photo captures were >60 minutes apart (i.e., ≥ 2 coyote captures within a 60-minute time span were treated as a single individual/capture event) (Tobler et al. 2008). All statistical analyses were conducted in R version 3.2.2 (R Core Team, 2016). To compare coyote attraction to different sensory cues, we used generalized linear mixed models (GLMMs; glmer function in package lme4) with counts of unique individuals as the dependent variable and sensory cue as the fixed effect. All GLMM's were defined to have a Poisson error distribution with a standard link function, an offset term (days sampled) to account for differences in the time each camera was active, and a random effect for transect (assuming varying intercepts and fixed slope) to account for non-independence of points within transects and variation among transects. To assess significance ($\alpha = 0.05$) of the sensory cue fixed effect, we used a likelihood ratio test to compare the above model to the respective null model (i.e., an intercept-only GLMM with the same error structure, offset term, and random effect). Upon finding the fixed effect to be a significant predictor of detection and attraction, we examined differences among treatments using a Tukey HSD test for pairwise comparisons (glht in package multcomp), with significance assessed after applying the False Discovery Rate (FDR) control.

Results

For remote trail-camera surveys, 51 total days were sampled in fall 2016, resulting in 552 total camera-days (264 for Cookson WMA and 288 for Nickel Preserve). At one visual cue station, a coyote completely removed the dove decoy; we attributed the 9 affected camera-days and 3 corresponding coyote captures to the control treatment because no cue was present. We

also censored 7 camera-days from analyses, including 1 from the visual cue and 6 from the olfactory-visual cue (all from Cookson WMA) because the visual cue was knocked to the ground. Thus, 545 total camera-days remained for analyses (olfactory: 140; visual: 130; olfactory-visual: 134; control: 141). For this sample of camera-days, at least 61 individual coyotes were recorded (7 from Cookson WMA and 54 from Nickel Preserve) from 44 unique capture events (i.e., photos). Ten capture events contained two individual coyotes, two captures contained three coyotes, one contained four coyotes, and all remaining captures contained one coyote each.

Likelihood ratio tests relative to the null model indicated that sensory cue was a significant predictor of the number of individual coyote captures ($\chi^2 = 247.4$, $df = 3$, $p < 0.001$). A Tukey's HSD test revealed that coyotes were equally detected and attracted to olfactory- and visual-only cues ($p = 0.27$), and that both of these single cue treatments attracted more coyotes than either the olfactory-visual cue or the control treatment ($p \leq 0.01$) (Fig. 3). Additionally, the olfactory-visual cue attracted significantly more coyotes than the control ($p < 0.001$). In other words, olfactory- and visual-only cues attracted the most coyotes followed by the combined olfactory-visual cue, followed by the control (i.e., olfactory = visual > olfactory-visual > control).

Discussion

Contrary to our first hypothesis, we provide evidence suggesting that coyotes equally use olfactory and visual sensory cues while foraging in forests. This finding of equal visitation at olfactory and visual cues is unexpected because past studies have suggested that this apex predator uses visual cues more than olfactory and auditory cues (Wells 1978; Wells and Lehner

1978; Baker et al. 2011). Unlike these earlier studies, which were conducted in a more controlled setting (e.g., an outdoor arena with live prey and sensory cues actively controlled), ours was the first to experimentally assess detection and attraction of free-roaming coyotes to sensory cues in a field setting. Because it is difficult to simulate and accurately characterize long range detection and attraction techniques with captive-held predators in laboratory studies, field studies provide important complementary insight into foraging strategies, as well as information that is directly applicable to understanding predator foraging behavior and sensory ecology more broadly.

Also unexpected relative to our second hypothesis, coyote visitation to a combined olfactory-visual treatment was lower than for the separate visual and olfactory treatments, although greater than for a no-cue control. We are not entirely certain of the explanation for this pattern, but one possibility is that coyotes were wary of the combined-cue treatment setup, which included both a dove decoy (visual) and visible scent drip (olfactory) located directly above the decoy (Fig. 2). This treatment may have appeared more visible and/or artificial than either cue by itself, which could have prevented coyotes from approaching or being captured in camera frames. Future research could test combined sensory cues that include an invisible olfactory component, such as liquid scent applied directly to a visual cue or scent tablets placed on the ground and obscured by litter or vegetation. However, these approaches may have the associated trade-off of reduced life of the scent, especially under wet conditions, compared to the ~2 weeks of scent life we achieved using scent drips, regardless of weather conditions.

In combination with previous studies suggesting that coyotes preferentially use visual detection under some circumstances (Wells and Lehner 1978; Wells and Bekoff 1982), our finding of an apparent equivalent use of olfaction and vision suggests that this apex predator is capable of using multiple sensory cues while foraging. The context-dependent use of multiple

sensory cues could improve foraging success when the conspicuousness of either visual or olfactory cues is reduced by environmental conditions. For example, when vision is restricted (e.g., at night), predators may rely more heavily on olfactory and auditory cues than during periods when visual cues are readily available (e.g., during the daytime) (Wells and Lehner 1978). Given our study design and relatively low replication of individuals captured, we were unable to identify whether spatiotemporal differences in the use of sensory foraging modes occur for coyotes in our study area, for example between locations and time periods of high and low visibility (e.g., daytime versus nighttime; foggy versus clear conditions; densely vegetated versus open areas; complex vs. level topographies) or between periods with different values of airflow conditions that influence olfactory detectability (humidity and wind velocity, turbulence, and updraft) (Fogarty et al. 2018). However, we hypothesize that such spatiotemporal differences in the use of sensory cues exist, and if so, this would help explain the difference between our findings, which were based on observations across a variety of conditions and times of day, and those of laboratory studies that may have captured only a subset of possible conditions.

The sensory mechanisms that predators use when foraging also have implications for prey avoidance behaviors, which in turn have ramifications for life history evolution and evolutionary “arms races” between predator and prey species (Dawkins and Krebs 1979). Our study provides insight into the use of sensory cues by the coyote, an apex predator that depredates many prey species, exerting both short-term behavioral and long-term selective pressures on prey to avoid being detected and depredated. Our finding that coyotes appear to use both olfactory and visual cues suggests that prey depredated by this species would benefit—in terms of both short-term survival and long-term fitness—by concealing or reducing both their olfactory and visual conspicuousness. Previous studies suggest that both olfactory and visual

concealment can provide such benefits to prey (Martin 1993; Vander Wall 2003; Carthey et al. 2011; Price and Banks 2016). Selection of visual concealment is well-documented for prey animals across a wide variety of vegetation cover types (Lima and Dill 1990); however, very little research has assessed how and whether prey can actively conceal their odors. To date, there is evidence that airflows characterized by high turbulence intensity rapidly disperse airborne odors making them difficult to track to a source (Conover 2007; Fogarty et al. 2018).

Whether animals are capable of perceiving and actively selecting such airflow currents as part of the broader habitat selection process is unknown. Some studies have provided evidence for such apparent selection for high levels of turbulence intensity (Conover and Borgo 2009) while others have not (Borgo and Conover 2016; Fogarty et al. 2017). These studies have focused on grassland and shrubland vegetation cover types, and prey selection of habitat for odor concealment is virtually unstudied in forests. Due to differences in prevailing airflow conditions between forests and these other cover types (Fogarty et al. 2018), we expect that predator use of olfactory foraging cues and prey selection for olfactory concealment is also likely to be different in forests compared to grasslands and shrublands. Therefore, even though our study indicates that an apex predator may equally use olfactory and visual cues in forests, different patterns of predator detection and attraction may occur in other vegetation types. For example, the relatively streamline (i.e., straight and invariant) airflow conditions typical of grasslands and other open areas are hypothesized to be more conducive to olfaction-based detection and tracking compared to forests, where airflows are more variable and less predictable (Fogarty et al. 2018). Future research should evaluate these potential foraging differences, as well as their implications to prey habitat selection and concealment strategies in different vegetation cover types.

Surprisingly few studies have investigated the relative use of different sensory cues by predators or compared sensory detection mechanisms among predator species, despite the expected importance of these mechanisms in driving short-term antipredator strategies of prey animals and long-term evolutionary arms races between predator and prey species. A first step toward a meaningful understanding of these broad classes of predator-prey interactions is understanding how predators use sensory cues while foraging. Here, we provide evidence for the use of both olfactory and visual sensory cues by an apex predator, which we hypothesize should drive antipredator behavior for a suite of prey species in forest ecosystems. Additionally, our study design represents a simple framework that can be used—and modified to capture different predator and simulated prey species—to experimentally examine predator use of sensory cues.

Future research is required to shed light on the general approaches by which predators detect prey and to parse apart the sensory processes used for the initial detection of prey items and for tracking of prey odors to the source after initial detection. Research should also investigate implications of predator detection mechanisms for the conservation management of both predator and prey species (Madliger 2012). For example, anthropogenic alteration of vegetation structure (e.g., due to fire suppression, altered grazing regimes, woody plant encroachment, deforestation and afforestation, and planting of windbreaks and tree plantations) can affect visibility, airflow, and acoustic and microclimate conditions, which underlie the prevalence and potency of multiple prey sensory cues (Vander Wall 1998; Conover 2007; Carroll et al. 2016). However, it remains unclear how such changes influence predator and prey interactions and population dynamics through changes in these multiple sensory cues. Finally, field research could expand beyond focusing on single predators to also evaluate and compare sensory detection modes used across the entire predator community. Because many prey species

are depredated by multiple predator species, each of which may employ an alternative sensory detection strategy, this community-level perspective would clarify the full suite of pressures driving prey habitat selection strategies and therefore provide a more comprehensive understanding of predator-prey interactions.

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Figure 1. Location of study area in Oklahoma, USA (A-B) and the (C) Nickel Preserve and Cookson WMA sites in the Cookson Hills of eastern Oklahoma, the westernmost extension of the Ozark Plateau.

Figure 2. Combined olfactory and visual sensory cue used in field experiment assessing use of visual and olfactory sensory cues by coyotes (*Canis latrans*). The visual cue treatment excluded the olfactory scent drip (the camouflaged container above the dove decoy), and the olfactory cue treatment excluded the dove decoy. Field experiments were conducted during fall of 2016 at Cookson WMA and Nickel Preserve, in eastern Oklahoma, USA.

Figure 3. Medians, interquartile ranges, and outliers for counts of unique coyote (*Canis latrans*) visits to trail cameras with each sensory cue treatment during fall of 2016 at Cookson WMA and Nickel Preserve, in eastern Oklahoma, USA.

Figure 1

Figure 2

Figure 3