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Point-of-view

Some important overlooked aspects of odors in avian nesting ecology

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Although outdated opinions about poor avian olfaction have largely disappeared in recent decades, there has been inadequate attention paid to olfaction of other organisms that interact with birds and their nests. In particular, olfaction is likely more important than vision for many biting arthropods and for many reptilian, mammalian, and likely even some bird predators of nests (e.g. some procellariiforms, piciforms, and corvids), but crypsis (or attractiveness) of nest odors has largely been ignored in the literature. Given the pivotal importance of nest success to a bird's fitness, there has likely been strong selection to conceal inadvertent cues to nest locations, including odors. Here, I summarize what is known about this, and discuss a few important topics I deem worthy of deeper investigation.

Keywords: GCMS, olfactory concealment, predation

Introduction

Evidence is fairly compelling that olfaction is a key sense of many animals, and substantial effort is invested in understanding how animals such as insects use it to find food and mates (Conover 2007). For most birds, however, the evidence is fairly compelling that vision is their key sense (Martin 2017). Consequently, most research on avian sensory ecology has been vision-centric, although there is also a substantial literature on sound detection and production (Martin 2017). These foci have certainly advanced our understanding of how birds use and produce visual and acoustic information, but they have likely also blinded us to other aspects of avian ecology, including olfaction (for finding food, navigating, etc.; for a sample of studies that illustrate olfactory abilities of birds see Bang and Wenzel 1985, Healy and Guilford 1990, Gagliardo 2013, Martin 2017, Grieves et al. 2019 and references therein). An important outcome of a vision- and sound-centric mindset has been that most of us have never even considered how birds and other taxa in a community may intercept olfactory cues produced by birds, and in particular their nests. Here, I briefly review avian olfactory ecology from a nest predator's perspective, and I highlight some areas of research that have received limited attention.

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Nest crypsis

A crucially important aspect of avian reproductive strategies is to avoid nest predation; one of the riskiest times in a bird's life is when they are inside a nest, whether it be as an egg, a nestling, or a parent (Ricklefs 1969, Martin 1995, Ibáñez-Álamo et al. 2015). One strategy is to make nests more cryptic, which is often tested based on human assessments of visual and acoustic cues (Briskie et al. 1999, Clark and Shutler 1999, Ruxton 2009, Tomás and Soler 2016). However, many biting arthropods, most reptilian and mammalian predators, and probably some avian predators of nests, likely rely more on olfaction than vision (Rangen et al. 2000, Conover 2007, Soini et al. 2007, Hughes et al. 2010). The bottom line is that many organisms that can harm birds likely use odors to find the latter. This means that there has almost certainly been strong selection for birds to limit detection of those odors, but there has been little research devoted to this. Similarly, it is perhaps surprising that more attention has not been devoted to considering how biting arthropods and predators of birds' nests use odor cues.

A first general strategy birds might use for limiting detection of nest odors is to reduce their production, which originate from adults, eggs, nestlings, and nesting material (Hagelin 2007, Karlsson et al. 2010, Amo et al. 2012, Webster et al. 2015, Golüke et al. 2016). Each of these will in turn be influenced by avian genes, diet, habitat, and microbiomes (Maraci et al. 2018). Crypsis of bird odors might be achieved by lowering metabolism while at nests (Conover 2007) and removing sources of odors such as via removal of fecal sacs (Thomson 1935, Wible 1960, Gill 1995). Lower metabolism has the drawback of generating less heat to incubate or brood, and for nestlings of slowing and impairing development (DuRant et al. 2013), which also lengthens the interval over which young are vulnerable in a nest to predators. Removal of fecal sacs has the drawback of attendant energetic costs (Weatherhead 1984). Alternatively, birds may have adaptations to change the types of odors they produce when nesting (Conover 2007, Moreno-Rueda 2017, Grieves 2019 and references therein). In support of this, Reneerkens et al. (2005) discovered that less volatile preen waxes were produced by shorebirds during reproduction. They subsequently showed that a domestic dog *Canis lupus familiaris* had more difficulty locating sources of these waxes of lower volatility.

A second general strategy birds might use for limiting detection of odors is to conceal their source. One way this could be achieved is if birds selected items that masked odors, such as specific kinds of vegetation or dung (Lafuma et al. 2001, Levey et al. 2004, but see Smith and Conway 2007, 2011). Birds do use volatiles against nest parasites (Wimberger 1984, Clark and Mason 1987, Mennerat et al. 2005, Shutler and Campbell 2007, López-Rull and Macías García 2015 and references therein), but whether they choose plants to conceal nests, to my knowledge, has not been tested. Currently, evidence for this kind of chemical camouflage in general is limited and ambiguous (Ruxton 2009). Another way birds could make nests less detectable by predators would be to situate nests in locations that more rapidly dissipate odors. Conover (2007) laid down a foundation for incorporating olfaction into studies of nesting ecology, and proposed the olfactory concealment hypothesis (Soini et al. 2007). Conover (2007) detailed how olfactory concealment could be achieved by nesting in locations that, for example, had greater turbulence, making it more difficult to trace origins of nest odors. Alternatively, some locations may more effectively cause odors to be diverted above the height at which, for example, a fox's *Vulpes* spp. nose occurs. Conover (2007, p. 71) provided experimental evidence that turbulence could throw a predator (he used a domestic dog) off a scent trail. I used Google Scholar™ to identify 136 publications that have cited Conover (2007) as of September 2018, and I checked the reference sections of relevant papers in that list. I found only six studies (Conover and Borgo 2009, Conover et al. 2010, Soanes 2015, Borgo and Conover 2016, Fogarty et al. 2017, 2018) that evaluated whether birds chose nest sites that offered olfactory concealment, although several authors have mentioned it as a consideration (Storaas 1988, Webb et al. 2012, Young et al. 2017). Conover and Borgo (2009) tested if loafing locations of adult sharp-tailed grouse *Tympanuchus phasianellus* provided optimal olfactory versus optimal visual concealment. They found that visual concealment of loafing sites did not differ from random sites, whereas olfactory concealment was greater at loafing than random sites. In contrast, Conover et al. (2010) found that greater sage grouse *Centrocercus urophasianus* used visual but not olfactory concealment at their nests; in fact, turbulence was lower at nest than random sites. Moreover, there was no difference in either visual or olfactory concealment for successful versus unsuccessful nests. In experiments where inactive crimson finch *Neochmia phaeton* nests were baited with Japanese quail *Coturnix japonica* eggs, Soanes et al. (2015) found no difference in predation rates of nests that contained no or some feces. Borgo and Conover (2016) similarly found no difference in olfactory concealment between waterfowl (pooling seven species) nest sites and random sites, but they did find that successful nests had better olfactory concealment. Fogarty et al. (2017) found no difference in olfactory concealment of northern bobwhite *Colinus virginianus*, eastern meadowlark *Sturnella magna*, or grasshopper sparrow *Ammodramus savannarum* nests versus random sites. Finally, Fogarty et al. (2018) provide data illustrating that artificially scented northern bobwhite eggs in open habitats (grass- and shrublands) survived better in areas with greater turbulence and uplift.

Birds may also circumvent crypsis, and use chemical defenses against predators and biting arthropods (Dumbacher et al. 1992, Douglas et al. 2004, 2005, Canestrari et al. 2014, Trnka et al. 2016, Moreno-Rueda 2017), producing substances that are noxious or toxic to predators. This has scarcely been evaluated, and in a very limited number of species (Dumbacher and Pruett-Jones 1996).

In sum, there has been extremely limited assessment of whether and how birds protect their nests from olfactory detection. Given the clear costs of predation, one can generate several predictions about where odor concealment may be best developed. Because odors dissipate more readily in the vertical plane for above ground nesters (Conover 2007), ground nesters appear to be the taxa worth investigating in the most detail, but it would be worthwhile to have data from above-ground nesters for comparison. I outline both a reductionist and holistic approach to tackling these questions.

A reductionist approach: which odors?

Odors that may give away nest locations include those of incubating females, eggs, nestlings for altricial birds, and substances produced by nest occupants, chiefly feces, particularly for altricial birds, but also for precocial species that defecate at nests (Conover 2007, Ibáñez-Álamo et al. 2014; reviewed by King and Shutler 2010). Very little research effort has been devoted to identifying odors that predators use to find nests (but see Whelan et al. 1994, Clark and Wobeser 1997, Reneerkens et al. 2005, Mihailova et al. 2018). Given that olfactory cues are likely used by predators to find nests, one might predict that predation rates would increase with nest age as odors accumulate. However, timing of predation can be random or decrease with nest age (Grant et al. 2005, Bulluck and Buehler 2008, Grant and Shaffer 2012). One reason a predation versus nest age hypothesis is not supported may be that adults have increased willingness to defend older young; however, parental defense by most species of birds against most predators is ineffective and even highly risky (reviewed by Montgomerie and Weatherhead 1988, also see Brown and Brown 1996). Another reason a predation versus nest age hypothesis is not supported may be that intensity of odors asymptotes early in the nesting stage; again, data are lacking. Yet another reason may relate to the predator community; some may be egg specialists and other nestling specialists; relative density of those predators will affect timing of predation. And finally, fecal odors may be unattractive to predators, although there is limited support for this latter hypothesis (reviewed by King and Shutler 2010).

Until recent decades, methods to quantify the distribution and concentration of olfactory cues were limited. Now, gas chromatography mass spectrophotometry (GCMS) has become commonplace (Soini et al. 2013), although it can be quite fidgety. Odors of interest are adsorbed onto a suitable substrate or absorbed into solvents. These are then heated to volatilize target odors. More volatile compounds, such as alcohols, are first to appear on the GCMS output which is a series of peaks over time. Heights of peaks indicate how much of a compound is present. The MS part of the procedure is to blast the substances in the sample with electrons, breaking them into smaller units, the mass of which is measured. To figure out how the pieces were initially joined together in the original compound(s), computers, standardized databases [e.g. NIST (2017)], various indices [e.g., Kovats retention index; Van den Dool and Kratz (1963)], and comparison with analytical standards are all used.

If one succeeds in identifying all odorants (= individual substances as opposed to mixtures) produced at nests, the next step is to partition out in controlled laboratory settings the ones that predators use. I am unaware of any research that has yet attempted this.

A holistic approach: can living predators identify active nests?

If one is simply interested in testing whether certain nests are more cryptic olfactorily, one could avoid detailed chemical analyses, and use choice tests with living predators (Rangen et al. 2000). Tests could include, for example, predator responses to nests of the same species that differed in age, that were inactive versus active, or comparisons among different prey species' nests. There are thus numerous questions that could be addressed with this approach.

Additional questions

Once we have data from both reductionist and holistic approaches to the questions raised above, and we are some years before that happens, we will be in position to test several important questions. Selection for olfactory concealment has almost certainly occurred in a variety of avian and non-avian taxa. Regardless, if it occurs, how is olfactory concealment achieved? For example, have seabirds that nest on islands free of reptilian and mammalian predators foregone olfactory concealment of their nests? Does olfactory concealment differ between large above-ground nesting species that may be more able to defend against predators, versus underground-nesting species (e.g. Leach's storm-petrel, *Oceanodroma leucorhoa*) that may be tracked down by olfactory predators? Indeed, many seabirds are well known for their distinctive odors (Humphrey and Phillips 1958, Warham 1990, 1996), although those odors may serve other functions, such as mate attraction (Hagelin 2007, Amo et al. 2012).

If we focus just on species that are targeted by olfactory predators, how different are nest odors that are produced among members of communities of prey species? How different are nest odors within species? Has there been convergent or disruptive evolution among species to conceal odors? Within predator communities, to what extent do species differ in the odors they use to detect nests? And again, how different are conspecific predators in the odors they use to find nests? The preceding questions are just a tip of an iceberg; my suspicion is that this area of research will soon blossom.

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