

EFFECTS OF OLFACTORY CUES ON ARTIFICIAL-NEST EXPERIMENTS

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ABSTRACT.—We examined the effects of two potential olfactory cues on the outcome of experiments using artificial nests to assay predation on open-cup nesting songbirds. In two experiments lasting 15 days each and replicated two times at three sites, bamboo nests baited with Japanese Quail (*Coturnix japonica*) eggs were placed on the ground in a 5 × 4 grid array with 50 m between adjacent nests. Egg survivorship was monitored every five days, and remote cameras were used to take photographs of animals removing bait eggs from nests. One experiment consisted of four treatments that varied the type and amount of olfactory information provided by the investigator: (1) human scent; (2) "no scent"; (3) "deer scent"; and (4) perfume. Artificial scents were applied to shoes, clothing, and skin during the experiment set-up and monitoring. For the first experiment, rates of nest loss were greater for the human-scent treatment than deer-scent and/or no-scent treatments in one-half of the spatial/temporal replicates. Rain appears to have complicated the effects of the scent treatments in some of the spatial/temporal replicates. Final levels of nest loss, however, were greater for perfume and human-scent treatments than deer-scent and no-scent treatments regardless of spatial/temporal replicate. The second experiment consisted of two treatments, one in which eggs were replaced periodically, and the other in which eggs were not replaced for the duration of the experiment. Both treatments had similar rates and final levels of nest loss. Approximately 90% of 51 photographs were of olfactory-searching, predominantly nocturnal mammals. We conclude that olfactory-searching predators can cue on human odors left in the area of artificial nests, but that either rain or scents (e.g. the deer scent) can be used to decrease this potential bias. In contrast, changing egg qualities over the time scale of our experiments do not provide additional cues to predators. Received 20 April 1992, accepted 25 November 1992.

ALTHOUGH NEST PREDATION has long been recognized as a major source of reproductive failure in bird species (e.g. Ricklefs 1969), only recently has nest predation been hypothesized to be an important determinant of bird community structure (Martin 1988a, b). Predation on eggs and nestlings may regulate bird populations (George 1987), influence habitat selection (Blancher and Robertson 1985), and affect patterns of nest dispersion and species coexistence (Martin 1988a, b). Perhaps more importantly, nest predation also may be important for the conservation of many bird species (Ambuel and Temple 1983, Wilcove 1985). In the increasingly fragmented landscapes of North America, nest predation may be an important contribution to population declines of many open-nesting bird species, particularly long-distance Neotropical migrants (e.g. Terborgh 1989).

One major methodological problem in studies of nest predation is finding enough nests of a given bird species to have meaningful sample sizes and to control possibly confounding vari-

ables (e.g. see Reitsma et al. 1990). Largely because of these methodological difficulties, investigators have been using artificial nests baited with quail eggs and have measured egg survivorship over some period of time simulating a normal incubation period (e.g. Andersson and Wiklund 1978, Loiselle and Hoppes 1983, Wilcove 1985, Martin 1987, Yahner 1989, Reitsma et al. 1990). Despite the growing use of artificial nests and the admission that some results from using these nests do not mimic results from real nests (e.g. Reitsma et al. 1990, S. A. Temple pers. comm.), few studies have examined in detail methodological issues involving the use of artificial nests. Martin (1987), for instance, reported that artificial wicker-basket nests had lower rates of nest predation than artificially baited real nests when both nest types were placed off the ground, but that artificial and real nests had similar rates of predation when placed on the ground. He concluded that the off-ground nests are found primarily by visual-searching predators and that these predators possibly avoid

artificial nests (T. E. Martin pers. comm.); also, he judged that ground nests are found primarily by olfactory-searching predators who do not respond to nest appearance.

Other investigators have questioned the extent to which olfactory-searching predators find artificial nests, thus questioning the biological relevance of the results of experiments using artificial nests (Willebrand and Marcström 1988). If artificial nests are seldom found by olfactory-searching predators, their reflection of predation pressures on real nests may be minimal. When a large olfactory-searching predator (e.g. a raccoon, *Procyon lotor*) finds a songbird nest, there is little possibility for the parents to drive off the predator (see Pettingill 1976). Even small songbirds, however, can sometimes drive away small, visual-searching predators like Blue Jays (*Cyanocitta cristata*) and eastern chipmunks (*Tamias striatus*; C. J. Whelan pers. obs., R. T. Holmes pers. comm.).

Artificial nests provide an attractive, nondestructive test system for examining nest predation. While use of artificial nests remains controversial, they do allow experimental control over numerous confounding factors like nest shape, height, density, position within a plant, and number of eggs. Therefore, the usefulness of artificial nests in understanding the importance of nest predation needs to be evaluated. Here we report the results of experiments designed to test specifically the potential for olfactory-searching nest predators to find artificial nests when these nests are carefully hidden on the ground under vegetation. We used two complementary experimental test systems that: (1) clearly indicated whether or not olfactory-searching predators find artificial nests; and (2) examined two possible methodological biases (human-scent trails and egg age/odor).

STUDY SITES AND METHODS

Experiments took place from May through August 1991 at three separate sites about 25 to 65 km west of Chicago, Illinois: (1) the Morton Arboretum (Lisle, Illinois); (2) Hawthorn Hill (Woodridge Park District, Woodridge, Illinois); and (3) the Elburn Forest Preserve (Elburn, Illinois). All three sites consisted of isolated tracts of eastern deciduous forest dominated by various oaks (*Quercus* spp.), sugar maple (*Acer saccharum*), white ash (*Fraxinus americana*), and a variety of shrubs and understory tree species (e.g. ironwood, *Ostrya virginiana*). The Morton Arboretum and Hawthorn Hill are surrounded by suburban homes, but

the Elburn Forest Preserve is surrounded by agricultural fields (mostly corn or soybeans). Olfactory-searching predators at these sites include the southern flying squirrel (*Glaucomys volans*), Virginia opossum (*Didelphis marsupialis*), raccoon, coyote (*Canis latrans*), red fox (*Vulpes vulpes*), and striped skunk (*Mephitis mephitis*), as well as domestic dogs (*Canis familiaris*) and cats (*Felis catus*).

Effect of human scent trails (experiment 1).—Human scent associated with artificial nests and eggs could serve as an olfactory cue that could lead to extremely biased estimates of nest predation (Reitsma et al. 1990). This experiment consisted of four treatments designed to differ in the extent of olfactory information supplied to potential predators. Each treatment consisted of 20 bamboo, wicker nests arrayed on a 5 × 4 grid system, with 50 m between adjacent nests (density 6.67 nests/ha). Each nest was lined with leaf litter and placed in a hole in the ground with the top of the nest flush with the soil surface. Nests were baited with two Japanese Quail (*Corturnix japonica*) eggs, and were examined for egg survivorship at days 5, 10, and 15 following placement in the field, conforming to a monitoring schedule used by Reitsma et al. (1990). The experiment was conducted twice, once in late May and once in early July. Scent treatments were switched among grid locations at each site for each time replicate. A single replicate of each treatment was conducted simultaneously at each experimental site, for a total of three replicates of each treatment both times the experiment was conducted.

Treatments consisted of: (1) human scent; (2) "deer scent" (Tink's # 69 Doe-in-Rut Lure); (3) "no scent" (Scent Shield and Scent Walker® Boot Pads); and (4) perfume (Primo). The human-scent treatment served as a basis for comparison with previous studies and was established by putting nests out on the grid in a standard fashion, walking from grid intersection to grid intersection, digging a slight depression in the ground, placing the nest in the hole, lining the nest with leaves, and baiting the nest with two quail eggs. Following Reitsma et al. (1990), we rubbed our hands with leaf litter prior to handling nests or eggs to decrease the amount of human scent left on or near the nest. Deer scent supposedly consists of white-tailed deer (*Odocoileus virginianus*) doe hormones, bodily secretions, and urine (but see Trost 1989); it can be simulated using ammonia and water (Trost 1989). Scent Shield and Boot Pads (used in the no-scent treatment) are designed to eliminate or to mask human scent. For each nonhuman-scent treatment, shoes, clothes, and skin were treated with the animal scent, masking scent, or perfume. Otherwise, nests were treated similarly to the human-scent treatment. Because of severely degraded habitat, part of the Hawthorn Hill site was unusable. Therefore, at Hawthorn Hill we used only three scent treatments: human scent, no scent, and perfume.

Two types of complementary data were collected

and analyzed: rates of egg survivorship (i.e. speed at which eggs disappeared) over the 15-day simulated "incubation period," and the final level of overall predation (i.e. number of eggs remaining at last census). Rates of predation at each site for each time replicate were analyzed with survival analysis (Benedetti et al. 1990). Final levels of predation (number of nests surviving at end of 15-day incubation period) were analyzed with a log-linear model (Brown 1990) that examined simultaneously the effects of time replicate, site, and scent treatment on the number of nests surviving (for an example of these statistical analyses, see Whelan et al. 1991).

The expectation for this experiment was that if visual-searching predators are the major predators on artificial nests, then rates and final levels of predation should not differ among treatments. We assumed that olfactory-searching predators like raccoons are more likely to associate the presence of food with humans than with deer. Consequently, if these predators are more important, we assumed that the human-scent and perfume treatments should have greater amounts of predation than the deer-scent and no-scent treatments.

Effect of egg age and odor (experiment 2).—Unrefrigerated eggs that are not incubated can develop a rather strong odor with increasing age. Therefore, it is possible that the longer baited eggs survive, the greater will be their susceptibility to olfactory-searching predators (a concoction including rotten chicken eggs is a frequent bait used by mammal trappers; Joel S. Brown pers. comm.). Egg susceptibility should not change with egg age for visual-searching predators. Experiment 2 tested whether egg susceptibility increases as a function of egg age. The experiment consisted of two treatments, each of which had the same basic design as experiment 1 and was replicated at each experimental site. In the no-replacement treatment, nests were baited on the first day of the experiment, and surviving eggs were not replaced for the entire 15-day incubation period. In the replacement treatment, surviving eggs were replaced with fresh eggs on each census day. Experiment 2 was conducted twice in a staggered fashion with experiment 1. Statistical analyses were the same as for experiment 1. In experiment 2, if visual-searching predators are the most important predators on artificial nests, we expected no difference in rates and levels of predation between the two treatments. If olfactory-searching predators are the most important predators on artificial nests, we expected greater rates and levels of predation on the no-replacement treatment nests than the replacement treatment nests.

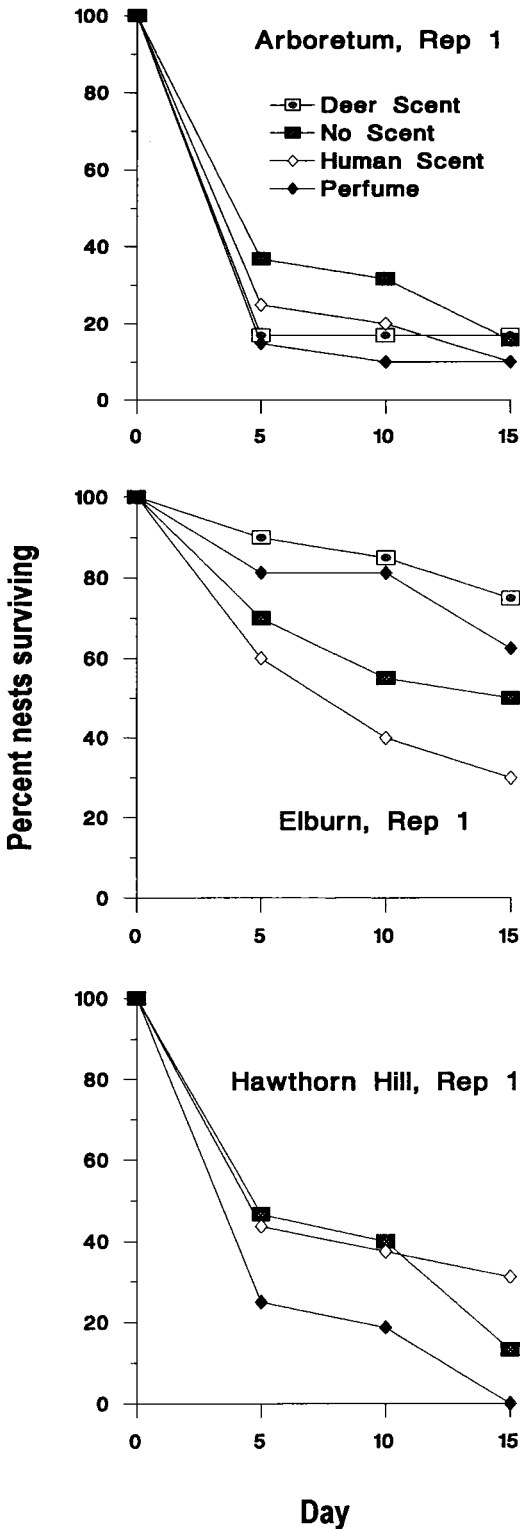
Remote-camera system.—In addition to the above experiments, remote cameras modified from Picman (1987; M. L. Dilger et al. unpubl. manuscript) were used to obtain pictures of predators taking eggs from the artificial nests. Each camera/nest setup consisted of a microswitch attached to an artificial nest that

electrically activated a solenoid mounted on the camera. When a bait egg was disturbed, the shutter was released. Cameras were placed along transects at the Arboretum and at Elburn, but not at Hawthorn Hill. The cameras were not placed on any of the experimental grids. Instead, transects were established away from the experimental grids using one of three scent treatments (human scent, no scent, or perfume), and five cameras were placed along each of these transects. Cameras were moved 5 m or more following a depredation event.

RESULTS

Experiment 1.—In the first time replicate there were significant differences in rates of nest loss among scent treatments only at the Elburn Forest Preserve. At this site, rates of nest loss increased from deer scent, to perfume, to no scent, and to human scent (Gehan-Wilcoxon test, $X^2 = 8.79$, $df = 3$, $P = 0.032$; Fig. 1). In the second time replicate, rates of nest loss differed significantly among the scent treatments at all three sites. Differences in rates of nest loss at both the Arboretum and Hawthorn Hill were close to our expectation if olfactory-searching predators were primarily responsible for nest losses. At the Arboretum, rates of nest loss increased from deer scent, to no scent, to human scent, and to perfume (Gehan-Wilcoxon $X^2 = 12.52$, $df = 3$, $P < 0.006$; Fig. 2). At Hawthorn Hill, rates increased from no scent, to human scent, and to perfume (Gehan-Wilcoxon $X^2 = 7.415$, $df = 2$, $P < 0.03$; Fig. 2). At the Elburn Forest Preserve, rates of nest loss differed among scent treatments, but not in the way predicted if olfactory-searching mammals are the important predators on these nests. Rates of nest loss at Elburn increased from human scent, to deer scent and perfume, and to no scent (Gehan-Wilcoxon $X^2 = 8.789$, $df = 3$, $P < 0.04$; Fig. 2). We found that on average 49.5% of nests (range 31–75%) in all treatments were chewed, were moved, or disappeared.

The log-linear model that best fits the multidimensional contingency table of time replicate, experimental site, scent treatment, and number of nests surviving included two interactions of main effects ($G = 32.41$, $df = 26$, $P = 0.180$). The interaction of scent treatment and number nests surviving ($G = 12.12$, $df = 3$, $P = 0.007$) indicates that final survivorship decreased from deer scent, to no scent, to human scent and perfume (Fig. 3). The three-way in-



teraction of time replicate, experimental site and number nests surviving ($G = 43.72$, $df = 2$, $P < 0.001$) indicates that the levels of overall mortality differed among the sites depending upon time replicate (Fig. 4). For instance, at the Arboretum, survivorship decreased moderately in the second time replicate. At Elburn, survivorship decreased dramatically in the second time replicate and, at Hawthorn Hill, there was virtually no difference in survivorship between time replicates.

Experiment 2.—There were no differences in rates of nest loss between the no-egg-replacement and egg-replacement treatments at any experimental site in either time replicate. The log-linear analysis of the multidimensional contingency table of experimental site, time replicate, replacement treatment, and number of nests surviving showed no significant main effects, nor any significant interactions of main effects. Indeed, virtually no nests survived at each site for each time replicate. On average 46.24% of nests (range 43–80%) in all treatments were chewed, were moved, or disappeared.

Remote-camera photographs.—Fifty-one photographs were taken showing eight different animal species. Most photographs (36) were of raccoons, regardless of scent transect. In several of these photographs, up to three different raccoons could be seen in the frame. The next most abundant animal photographed (7) was the Virginia opossum. Photographs of two other mammals, the eastern chipmunk and the white-tailed deer, were taken only on the perfume transect. Although the eastern chipmunk is primarily a visual-searching predator, it is also possible that it sometimes locates food using olfaction (D. Jedlicka pers. comm.). Whether the deer was actually preying upon the egg, or simply tripped the camera accidentally, is not evident from the photograph. The three photographs of a non-olfactory predator, the Blue Jay, were associated with the no-scent transects. Three of the photographs are of animals that probably tripped the cameras accidentally, an American Robin (*Turdus migratorius*), a Black-capped chickadee (*Parus atricapillus*), and an unidentified bird.

Fig. 1. Percent nests surviving over 15-day simulated incubation period for nests in four scent treatments for first-time replicate of experiment ($n = 20$ nests/treatment).

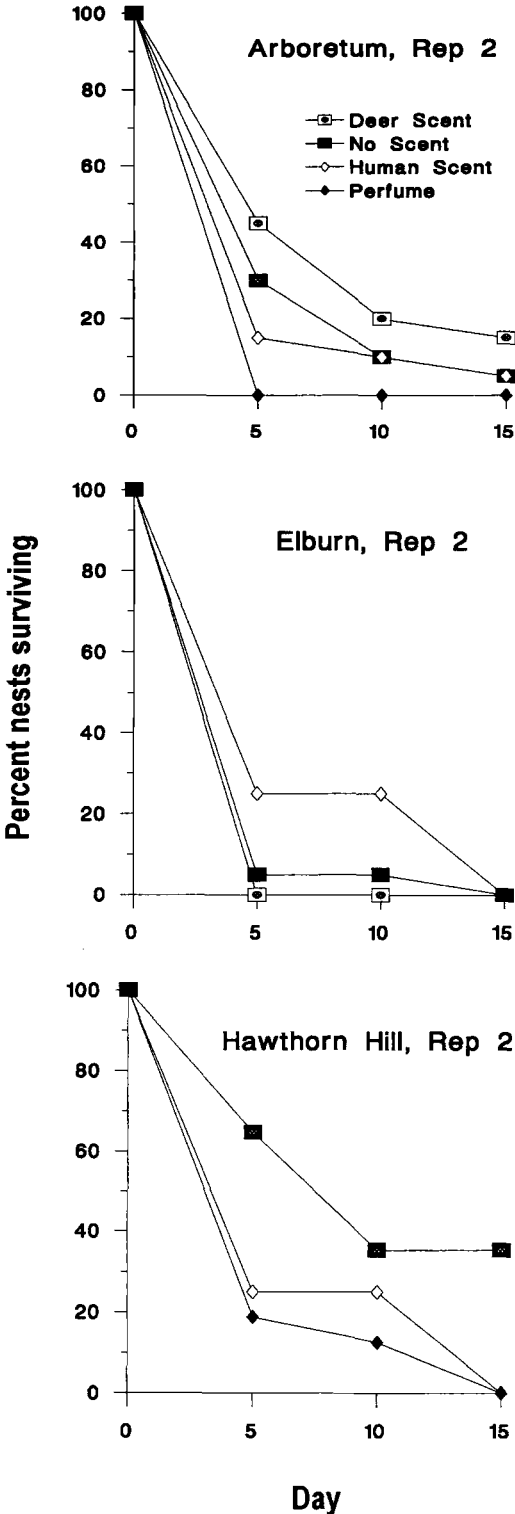


Fig. 2. Percent nests surviving over 15-day simulated incubation period for nests in four scent treat-

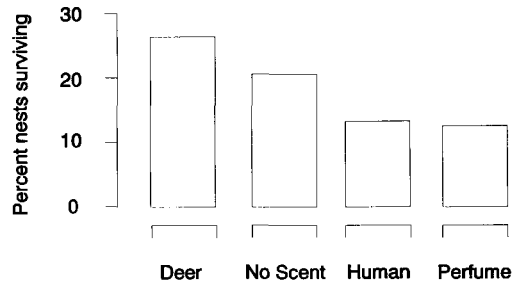


Fig. 3. For different treatments, percent nests surviving at completion of each time replicate for both time replicates combined ($n = 60$ nests/treatment, except for deer-scent treatment in which $n = 40$ nests).

DISCUSSION

Our results indicate that olfactory-searching mammals were the primary predators on artificial nests baited with quail eggs. In experiment 1 for one-half of the site/time replicates, the rates of predation were greatest for nests associated with human or perfume scent, and least for nests associated with no scent or deer scent. Nests in the deer-scent treatment had almost twice the final survivorship as those in the human and perfume treatments. Finally, about 90% of the photographs of animals attacking artificial nests were of olfactory-searching mammals. Of these, the raccoon is clearly the most important.

In contrast, there were no differences among treatments in experiment 2. According to original expectations, this would have been interpreted as evidence against olfactory-searching predators playing a major role in depredation of artificial nests. However, given the results of the remote cameras, coupled with the large number of nests that were chewed, were moved, or disappeared in both experiments 1 and 2, our original expectation for this experiment seems mistaken. If changing odor has no effect on egg susceptibility, or if egg odor does not change during the 15-day simulated incubation period, then there should have been no great differences between the two experimental treat-

ments for second-time replicate of experiment. Symbol for perfume scent is hidden by symbol for no scent in that their survival curves were identical ($n = 20$ nests/treatment).

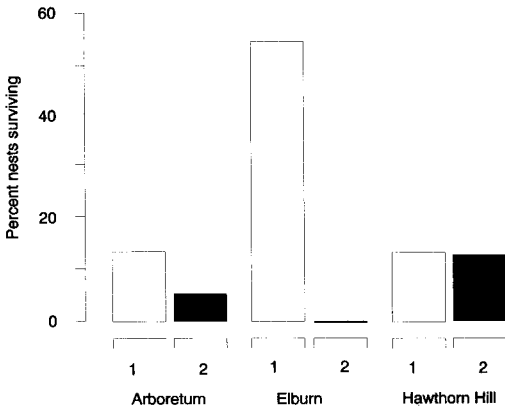


Fig. 4. Percent nests surviving according to both experimental site and time replicate ($n = 80$ nests \cdot [time replicate] $^{-1}$ \cdot [site] $^{-1}$ except Hawthorn Hill, for which $n = 60$ nests \cdot [time replicate] $^{-1}$ \cdot [site] $^{-1}$).

ments, regardless of whether predation is by olfactory-searching or visual-searching predators.

One striking result is the amount of variability in the rate of nest depredation among the sites and between time replicates for experiment 1. A likely explanation for this variability seems to be related to weather conditions, especially those conditions at the times the experiments were set up. At the time when the first time replicate was set up, northeastern Illinois (including each of the three sites) experienced a large, regional rain storm. The vegetation and ground at each site were extremely wet both when the nests were placed on the grid and, again, when they were baited with eggs. It seems possible that the rain decreased the effectiveness of the scents applied to shoes, clothing, and skin.

This interpretation is supported by the results of the second time replicate. Two of the sites (the Arboretum and Hawthorn Hill) remained dry during the course of the experiment. The Elburn Forest Preserve, however, experienced localized but extremely severe rainstorms, both when the nests were placed on the grids and when they were baited with eggs. At the two sites with dry-weather conditions, rates of nest loss were least for the deer-scent and no-scent treatments, and greatest for the human-scent and perfume treatments. In contrast, at Elburn, which was deluged by rain, there were significant differences among the scent treatments, but not in a way that is easily interpretable.

Thus, it is plausible that the confusing results of the first time replicate and the Elburn study site in the second time replicate can be attributed to confounding effects of rain.

If our results are interpreted to indicate that olfactory-searching predators are more likely to find artificial nests than visual-searching predators, it may be argued that these nests adequately assay for effects of olfactory-searching predators. However, our findings also suggest that olfactory-searching predators can use olfactory information supplied by the investigator and, thus, results from these experiments may actually overestimate the importance of olfactory-searching predators. There may be two ways to prevent such overestimation. First, because rain obscures or confounds whatever olfactory information is left in the neighborhood of the artificial nest by the investigator, one possible way to decrease the ability of olfactory-searching predators to cue in to that information is to set up the experiment during a rainstorm. Second, in dry-weather conditions, animal or shielding scents (as used in our experiments) could effectively mask the odor left by the investigator.

Perhaps the most important implication of our findings is that uniform methodology is essential for results of different studies to be comparable (e.g. Knight and Temple 1986). Different methodologies (e.g. frequency of nest monitoring) are likely to introduce different suites of biases, making comparisons problematic. In the future, if some investigators follow our lead in using animal or shielding scents to reduce the effects of investigator odor, they will need to use caution when comparing their results with studies that used no scents.

Just how olfactory-searching predators are responding to the scent treatments of experiment 1 is not clear, but two alternatives (not mutually exclusive) seem likely possibilities. First, the predator may detect a trail of scent left by the investigator, learn to associate this scent with an egg reward and, thus, "trapline" from nest to nest. Second, the scent treatments we used may simply increase the "radius of detection" of a nest (i.e. the extent of the area around a nest associated with a particular scent cue). If predators like raccoons are attracted to unusual scents (neophilia rather than neophobia), the greater the radius of detection, the higher the likelihood of nest depredation. Casual inspections of the temporal and spatial patterns of nest

losses in these experiments suggest that, in our systems, the second alternative is the more likely. Determining which, if either, of these alternatives is correct may be an important next step in understanding methodological intricacies of the experimental technique.

Our experiments indicate that it may be possible to vary experimentally the types of olfactory cues associated with nests and, thus, begin to determine which cues various predators are at least potentially able to use when finding nests. Experimental manipulation of visual cues, as well as various combinations of visual/olfactory cues, also may be possible. Such manipulations could reveal much about the sensory stimuli important to the success of nest predators, and this information could in turn suggest habitat manipulations that could decrease their impact on cup-nesting bird species.

Investigators studying avian nesting success have long been concerned that their presence and monitoring of nests could have negative consequences for individual birds under study (e.g. Bart 1977, Lenington 1979, Götmark and Åhlund 1984). Predators could be attracted to agitated parents, follow investigators visually, cue in to markers left near nests, or follow scent trails to the nest. Our results support the suggestion that olfactory predators potentially could use human scent to locate nests. Various ideas have been offered to counteract the potential bias caused by the presence of humans, including repellents (e.g. mustard oil and kerosene [Hammond and Forward 1956]; naphthalene moth balls [Hamerstrom 1970, Gawlik et al. 1988] and mechanical devices [Post and Greenlaw 1989]). As suggested above for artificial nests, the use of animal or shielding scents to mask human odor could be an important tool in studies of actual nesting success. Our findings indicate that any steps taken to decrease the amount of human scent in the proximity of nests should help to decrease the potential negative influence of observer presence.

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