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Authors: Edmunds, Sarah E., Kasparov, Christine N., Yoon, Jae Byeok, Kanonik, Alexandra K., and Burke, Russell L.

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Twelve Years Later: Reassessing Visual and Olfactory Cues Raccoons Use to Find Diamondback Terrapin Nests

SARAH E. EDMUNDS,[1,5] CHRISTINE N. KASPAROV,[2] JAE BYEOK YOON,[3] ALEXANDRA K. KANONIK,[4] AND RUSSELL L. BURKE[2,4]

[1]*Advanced Inquiry Program at Miami University/Wildlife Conservation Society, Bronx, New York 10460 USA*
[2]*Department of Biology, Hofstra University, Hempstead, New York 11549 USA*
[3]*35 Hampshire Road, Washington Township, New Jersey 07676 USA*
[4]*American Littoral Society, 18 Hartshorne Drive, Suite #1, Highlands, New Jersey 07732 USA*

ABSTRACT.—**As is true for many North American turtles, nest predation by Raccoons (*Procyon lotor*) is the primary cause of mortality of Diamondback Terrapin (*Malaclemys terrapin*) eggs laid at Jamaica Bay, New York, USA. Previous research using artificial nests at this site indicated that Raccoons located nests based on soil disturbance and ocean water scent, were repelled by human scent, and that vinyl marking flags did not increase predation rates. To test whether more than a decade of subsequent field work at the same site resulted in a change in Raccoon behavior, we replicated the previous 9 artificial nest experiments and added 4 new designs, for 13 total treatments. Our experiments further tested the effects of seven potential cues used for locating nests: moisture, human scent, Diamondback Terrapin scent, ocean water scent, fresh water scent, soil disturbance, and flag markers. Our results corroborate previous research that flag markers are not important cues for Raccoons to locate terrapin nests. Contrary to previous research, we found that ocean water scent no longer increases Raccoon predation and human scent no longer repels Raccoons. Also, in the first test of its kind, we found that Raccoons dug at sites where we applied geosmin, a pungent organic compound produced by Actinobacteria, which is naturally released when soil is disturbed. We conclude that Raccoons in Jamaica Bay have not learned to use signs left by humans and continue to locate nests primarily by relying on the tactile cue of soil disturbance rather than visual markers, moisture, or olfactory cues.**

In many turtle populations, nest predation rates are extremely high and can pose serious threats to the recruitment necessary for sustaining populations (Mitchell and Klemens, 2000; Spencer, 2002). Different predators may use different cues such as visual observation of nesting females, olfactory cues associated with the secretions of the nesting female during oviposition, presence of eggs, or visual or tactile disturbance of soil layers during nest digging (Wilhoft et al., 1979). Investigations of the cues that predators use to locate nests may provide insight not only into predator–prey ecology and evolution but also guide conservation measures and inform the way researchers collect data on turtle nests. As a result of the importance of this topic, numerous researchers have investigated the cues that predators use to detect turtle nests (e.g., Wilhoft et al., 1979; Tuberville and Burke, 1994; Galois, 1996; Burke et al., 2005; Rollinson and Brooks, 2007; Strickland et al., 2010; Geller, 2015; Oddie et al., 2015; Buzuleciu et al., 2016; Rutherford et al., 2016).

Every year since 1998, researchers have monitored and marked Diamondback Terrapin nests on the island of Ruler's Bar Hassock (RBH) in Jamaica Bay, New York, USA. In doing so, they have left behind cues such as vinyl marking flags (deliberately) and other human disturbances (unintentionally) at Diamondback Terrapin nests, items which may be used by predators to locate nests. Raccoons, the only detected predator of Diamondback Terrapin eggs or nests at RBH, regularly depredate 92–98% of nests at this site (Feinberg and Burke 2003; Burke and Kanonik, unpubl. data). To test the effects of various cues on Raccoon predation of Diamondback Terrapin nests, Burke et al. (2005) constructed artificial terrapin nests on RBH in 2003 and 2004. They were especially concerned that the vinyl surveyor's flags that researchers used to mark freshly oviposited Diamondback Terrapin nests might also facilitate nest predation by Raccoons. In addition to flag markers, Burke et al. (2005) investigated whether Raccoons used the cues of Diamondback Terrapin scent, human scent, ocean water scent, fresh water scent, and soil disturbance to find and predate nests. They concluded that Raccoons did not use flags to find nests and instead located nests based on soil disturbance and ocean water scent. They also found that Raccoons were repelled by human scent.

Raccoons are sophisticated problem-solvers, as demonstrated by their ability to learn rapidly (Dalgish and Anderson, 1979). Using food incentives, Davis (1984) showed they can master opening artificial objects such as clear Plexiglas cubes. In our study, 12 yr after Burke et al. (2005), we replicated their methods to construct artificial Diamondback Terrapin nests on RBH during the 2016 and 2017 Diamondback Terrapin nesting seasons. Our goal was to test whether the resident Raccoon population's predation behavior had changed after more than a decade of subsequent fieldwork at this site. By constructing various artificial nest designs as was done by Burke et al. (2005), we investigated the same combinations of natural and artificial cues Raccoons might use to locate Diamondback Terrapin nests including vinyl flags, Diamondback Terrapin scent, human scent, ocean water scent, fresh water scent, and soil disturbance. We also explored the possible effect of an olfactory indication of soil disturbance—the natural compound geosmin—as had been suggested by Geller (2015) and Buzuleciu et al. (2016).

Many researchers who study turtles and birds have explored the limitations of using artificial nests to study predation rates of real nests. Even carefully constructed artificial nests may still smell like humans and possibly serve as cues for predators to locate nests and/or bias the type of predators locating the nest. Rollison and Brooks (2007) noted that artificial turtle nests that do not contain turtle eggs are likely to have different predation rates than natural nests, as turtle eggs are likely an important cue for olfactory-oriented predators, though this has not been tested. However, some avian studies suggest that artificial nest predation rates may be valuable in detecting trends in predation rates (Wilson et al., 1998) as well as provide a useful tool for

[5]Corresponding Author. E-mail: edmundse@miamioh.edu
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FIG. 1. We studied Diamondback Terrapin nesting habitats on the island of Rulers Bar Hassock in Jamaica Bay Wildlife Refuge, New York, USA.

predicting the predation rates of potential reintroduction sites (Lewis et al., 2009). Additionally, Marchand et al. (2002) noted that some potential biases associated with artificial nests in avian studies (e.g., lack of parental care) do not apply to freshwater turtle studies.

MATERIALS AND METHODS

Like Burke et al. (2005), we conducted our studies in sand and mixed grassland Diamondback Terrapin nesting habitats on the island of Rulers Bar Hassock (RBH) in Jamaica Bay Wildlife Refuge, located in Gateway National Recreation Area, on the border of Kings and Queens Counties, New York, USA (40.615582°N, 73.833658°W; Fig. 1). At RBH, Diamondback Terrapin nesting season lasts about 6 wk, from early June to late July, and generally remains constant throughout this time period (Burke and Kanonik, unpubl. data). Our trials took place during the normal Diamondback Terrapin nesting season, from 11 June to 23 July 2016, and throughout July 2017. We created artificial nests mimicking the nine nest designs (called "treatments") of Burke et al. (2005), added a 10th treatment in 2016, and then 11th, 12th, and 13th treatments in 2017. Each treatment was designed to test a different variable on predation rates (see Table 1). We constructed artificial nests of various treatments simultaneously throughout each nesting season, interspersed with real terrapin nests. We monitored artificial nests for signs of Raccoon digging daily for 4 d following construction and considered the nests depredated if we identified signs of Raccoon digging anywhere between the nest marker flags (Burke et al., 2005).

Following the protocol of Burke et al. (2005), we measured predation rates of natural nests ($n = 42$) in addition to predation rates of artificial nests. To measure natural predation rates, we observed Diamondback Terrapins nesting, allowed them to finish without disturbance, and marked the nest sites with orange vinyl flags at 25 cm to either side of the nest, as researchers have done annually at this site since 1998. We monitored these nests for signs of predation daily for 4 d following oviposition and considered them depredated if the nest hole was excavated or empty egg shells were visible (Feinberg and Burke, 2003; Burke et al., 2005).

Our first artificial nest design, Treatment 1 ($n = 36$), served as a control for our other artificial nest experiments, as it most closely simulated a real terrapin nest. We wore surgical gloves to mask human scent (though future studies should explore whether latex gloves might themselves serve as an olfactory cue to Raccoons or other predators) and were careful not to kneel on the ground as we hand-dug artificial nest cavities. We excavated holes to 10 cm deep and 4 cm wide (approximately the width and depth of two fingers), comparable to the size of a natural Diamondback Terrapin nest. We placed orange vinyl surveyor's flags 25 cm to either side of the artificial nest cavity, typical of flagged nests at this site since 1998 (Feinberg and Burke, 2003; Burke, unpubl. data). We filled the cavities with a mixture of plain beach sand and Diamondback Terrapin-scented sand, which we created by placing an adult female Diamondback Terrapin in a container of beach sand for at least 30 min (Burke et al., 2005). We smoothed and patted down the filled-in nest surface with a gloved hand, again taking care to not kneel on the ground, mimicking the actions of nesting Diamondback Terrapins in making their nests inconspicuous.

For artificial nest Treatment 2 ($n = 16$) and Treatment 3 ($n = 16$), we placed flags farther from the hand-dug cavity to investigate whether Raccoons used flags themselves as visual cues to find Diamondback Terrapin nests (Burke et al., 2005). We constructed these nests identically to Treatment 1 nests except we placed orange flags 60 cm to either side of the nest for Treatment 2 and 100 cm to either side of the nest for Treatment 3. We followed Burke et al.'s (2005) assumption that flags at each of these distances would be too far apart to serve as reliable indicators of nest location to Raccoons.

Artificial nest Treatment 4 ($n = 25$) was designed to test whether Raccoons generalized an association with orange flags and nests (Burke et al., 2005). Raccoons are generally considered to be monochromatic, or colorblind (Michels et al., 1960), specifically with a single cone type in their retinas that allows for peak photopigment perception at the 560-nanometer wavelength (yellow-green light; Jacobs and Deegan, 1992). Replicating the Burke et al. (2005) original experiment, we used green flags instead of orange flags for this treatment, with all other conditions remaining the same as Treatment 1.

Artificial nest Treatment 5 ($n = 116$) was designed to test whether Diamondback Terrapin scent itself, as well as moisture, are cues to the presence of a Diamondback Terrapin nest (Burke et al., 2005). Instead of filling the excavated hole with a mixture of plain sand and Diamondback Terrapin-scented sand, we filled it solely with plain, dry beach sand. We constructed this treatment type otherwise identically to Treatment 1.

Artificial nest Treatment 6 ($n = 17$) was designed to test whether soil disturbance is still an important cue for Raccoons. This treatment tested whether orange flags alone, with no nest cavity, would be recognized as indicating the presence of a nest (Burke et al., 2005). For this treatment, we placed the flags 25 cm to either side of a randomly chosen, undisturbed spot, and added no other manipulations.

Artificial nest Treatment 7 ($n = 16$) was designed to test the effect of human scent on predation rates (Burke et. al, 2005). For this treatment, we did not wear surgical gloves while digging the nest cavity, and we mixed human saliva with beach sand to fill the hole instead of terrapin-scented sand. This treatment was otherwise identical to Treatment 1, with orange flags placed 25 cm to either side of the filled-in, smoothed-over cavity.

Artificial nest Treatment 8 ($n = 16$) and Treatment 9 ($n = 16$) were designed to test various scents as cues to nests (Burke et al., 2005). These treatments were identical to Treatment 6 in which we dug no nest cavity except we poured 50 mL of ocean

TABLE 1. Descriptions of artificial nest treatments and results of Diamondback Terrapins in Jamaica Bay, USA. N/A = Not Applicable

	Sample size 2016	Sample size 2017	Primary cue tested	Cavity present	Moisture present	Surgical gloves worn	Cue added to cavity	Cue added to surface	Flag color and placement	% depredated 2016	% depredated 2017
T1	36	39	Control for all other artificial nests	Yes	Yes	Yes	Terrapin-scented sand	None	Orange at 25 cm	92	74
T2	16	0	Flag distance	Yes	Yes	Yes	Terrapin-scented sand	None	Orange at 60 cm	81	N/A
T3	16	0	Flag distance	Yes	Yes	Yes	Terrapin-scented sand	None	Orange at 100 cm	81	N/A
T4	25	0	Flag color	Yes	Yes	Yes	Terrapin-scented sand	None	Green at 25 cm	80	N/A
T5	116	0	Moisture	Yes	No	Yes	Plain, dry beach sand	None	Orange at 25 cm	75	N/A
T6	17	39	Control for nests with no cavity	No	No	Yes	No cavity	None	Orange at 25 cm	6	3
T7	16	0	Human scent	Yes	Yes	No	Human saliva mixed with plain sand	None	Orange at 25 cm	88	N/A
T8	16	0	Ocean water scent	No	Yes	Yes	No cavity	50 mL ocean water	Orange at 25 cm	31	N/A
T9	16	0	Fresh water scent	No	Yes	Yes	No cavity	50 mL fresh water	Orange at 25 cm	38	N/A
T10	17	0	Terrapin scent in absence of soil disturbance	No	Yes	Yes	No cavity	100 mL terrapin-scented sand	Orange at 25 cm	47	N/A
T11	0	20	Geosmin scent	No	Yes	Yes	No cavity	0.1 mL of 0.5 mg geosmin/1 mL methanol solution	Orange at 25 cm	N/A	25
T12	0	19	Geosmin scent	No	Yes	Yes	No cavity	0.2 mL of 0.5 mg geosmin/1 mL methanol solution	Orange at 25 cm	N/A	37
T13	0	39	Control for geosmin nests	No	Yes	Yes	No cavity	0.1 mL of methanol only	Orange at 25 cm	N/A	0
Real nests	42	Not studied	Control	Yes	Yes	N/A	N/A	N/A	Orange at 25 cm	67	Not studied

water on a randomly chosen spot for Treatment 8 and 50 mL of fresh water on a randomly chosen spot for Treatment 9.

We added artificial nest Treatment 10 ($n = 17$) in 2016 to further explore the role of soil disturbance in predatory behavior. This treatment was designed to test whether Diamondback Terrapin scent alone, in the absence of an artificial nest cavity, would cause exploratory digging by Raccoons. As with Treatments 6, 8, and 9, we did not dig a nest cavity, and we placed orange flags 25 cm to either side of a randomly chosen, undisturbed spot within active nesting areas. We then poured 100 mL of Diamondback Terrapin-scented sand, created as described in Treatment 1, directly on top of these spots.

In July 2017, we added three additional treatments (Treatments 11, 12, and 13) to explore the role that geosmin might have on Raccoon predation behavior. We also repeated Treatment 1 (orange flags at 25 cm, hand-dug cavity filled with terrapin-scented sand) ($n = 39$) and Treatment 6 ($n = 39$) (orange flags at 25 cm, no cavity or scents added) as controls for these new treatments. For Treatment 11 ($n = 20$) and Treatment 12 ($n = 19$), we chose artificial nest sites as before and injected measured amounts of a 0.5 mg geosmin/1 mL methanol solution just under the surface of the sand substrate. For Treatment 11, we injected 0.1 mL of the solution at each site, and for Treatment 12 we injected 0.2 mL of the solution at each site. Then we put two orange flags 25 cm on opposite sides of each geosmin site. For Treatment 13 ($n = 39$), we repeated the Treatment 11 and 12 protocol except no geosmin was added to the methanol, so this served as a control for Treatments 11 and 12.

We built 447 total artificial nests between 2016 and 2017 (291 and 156 each year, respectively), comparable to the 448 total artificial nests that Burke et al. (2005) constructed between 2003 and 2004 (128 and 320 each year, respectively). While Burke et al. (2005) used a sample size of 16 nests per treatment in 2003 and 40 nests per treatment in 2004, we used a minimum sample size of 16 nests per treatment in 2016 and 2017. We used a lower minimum sample size in this study because of a unique factor in 2016: our colleague constructed more than 100 artificial terrapin nests for Treatment 5 ($n = 116$) as part of another predation study at the same site during the same time period (Czaja et al., unpubl. data). We were able to include this large sample for analysis in our study, but it limited the sample sizes of our other nest treatments because we wanted to avoid constructing too high a density of artificial nests overall, as we constructed our artificial nests in areas with multiple real Diamondback Terrapin nests.

We examined a 2×10 contingency table for significant heterogeneity among the 2016 artificial nest treatments using a goodness-of-fit test. Based on these results, we analyzed 14 comparisons: natural nests vs. all 10 artificial nest treatments and Treatment 6 vs. 5, 8, 9, and 10 to compare predation rates among artificial nests with no cavities. We analyzed these comparisons post hoc with repeated *G*–tests of goodness-of-fit with appropriate Bonferroni corrections.

We examined a 2×5 contingency table for significant heterogeneity among the 2017 artificial nest treatments using a goodness-of-fit test. Based on these results, we analyzed six comparisons: Treatment 11 vs. Treatments 1, 6, and 13, and Treatment 12 vs. Treatments 1, 6, and 13. We analyzed these comparisons post hoc with repeated *G*–tests of goodness-of-fit with appropriate Bonferroni corrections.

We were also concerned that nest predation rates might differ over the course of the 2016 nesting season from June to July, possibly because of Raccoons learning to identify artificial nests or improving their ability to locate real nests. Because Raccoons have switched from consuming only Diamondback Terrapin egg contents without shells early in the nesting season to eating entire eggs with shells later in the season (Feinberg and Burke, 2003; Burke et al., 2009), we anticipated a change in their behavior between June and July in this study as well. We compared artificial nest predation data and real nest predation data in June with data collected in July using two-tailed chi-square (χ^2) tests.

Results

There was significant heterogeneity among the artificial nest treatments in 2016 ($G_9 = 22.4$, $P = 0.008$). Only predation rates of Treatments 1, 6, and 8 were significantly different from predation rates of natural nests ($n = 42$). Treatment 1, designed to most-closely simulate a real Diamondback Terrapin nest, had the highest predation rate (92%), significantly higher than natural nests (67%; $G_1 = 12.7$, $P = 0.0003$). Both Treatment 6 (6% depredated, $n = 17$) and Treatment 8 (31% depredated, $n = 16$) had significantly lower predation rates than natural nests ($G_1 = 28.36$, $P < 0.0001$; $G_1 = 8.349$, $P = 0.0039$, respectively). Treatment 6 nests, for which we did not dig a cavity or add moisture or olfactory cues, had the lowest predation rate of all treatments (6% depredated, $n = 17$). Treatment 2 (81% depredated, $n = 16$), Treatment 3 (81% depredated, $n = 16$), Treatment 4 (80% depredated, $n = 25$), and Treatment 7 (88% depredated, $n = 16$) all had predation rates that were not significantly different from natural nests. Treatment 5 (75% depredated, $n = 116$), Treatment 8 (31% depredated, $n = 16$), Treatment 9 (38% depredated, $n = 16$), and Treatment 10 (47% depredated, $n = 17$) all had significantly higher predation rates than did Treatment 6 (all $P < 0.001$).

The levels of geosmin we applied in 2017 were sufficient to create an odor we could detect and, unlike either Treatment 6 (flags only) or Treatment 13 (methanol only) which had little or no predation, both of our geosmin treatments were depredated at moderate rates (Treatment 11: 25%, Treatment 12: 37%). There was significant heterogeneity among the artificial nest treatments in 2017 ($G_4 = 22.7$, $P < 0.0001$). The artificial nests with geosmin had significantly lower predation rates than did Treatment 1 (Treatment 11: $G_1 = 17.15$, $P < 0.0001$; Treatment 12: $G_1 = 12.22$, $P < 0.001$), but were not significantly different from any of the other controls (all $P > 0.14$).

Predation rates for real nests in June 2016 (74%, $n = 23$) did not differ from predation rates in July 2016 (58%, $n = 19$) ($\chi^2 = 0.32$, df = 1, $P = 0.57$). Predation rates for artificial nests in June 2016 (76%, $n = 101$) did not differ from predation rates in July 2016 (76%, $n = 189$).

Discussion

Raccoons are the most important predators of turtle nests in many places in North America (Mitchell and Klemens, 2000). Female Raccoons become reproductively mature at 1 yr and can live at least 5.8 yr at Jamaica Bay (Rulison, 2009), allowing the potential for 6 to 12 generations of Raccoons in a span of 12 yr (Zeveloff, pers. comm.). Female Raccoons teach their young how to forage by example (Zeveloff, 2002), and adults can successfully mimic behaviors of other Raccoons immediately after witnessing them acquire food (Shepherd, 1911). Dalgish and Anderson (1979) showed that Raccoons readily discover and exploit novel food sources, quickly learn to associate

environmental cues with food, and that these associations are broken slowly. This idea is further supported by Davis's (1984) finding that Raccoons can learn to discriminate between number cues; one individual that was initially exposed to a cube containing three food items and eventually to a wide array of cubes containing up to five items showed improvement in choosing the "correct" target three-cube with each successive trial.

Despite this evidence of Raccoons' impressive ability to learn, we found that marking artificial nests with flags did not affect predation rates by Raccoons, supporting previous experiments at this site 12 to 13 yr earlier (Burke et al., 2005). Artificial nests with only flag cues were rarely disturbed whereas artificial nest sites with flags plus soil disturbance were frequently depredated. The similarly high predation rates among artificial nests with flags at varying distances and of different colors (Treatments 1, 2, 3, and 4) indicates that Raccoons located these nests with nonvisual cues, perhaps tactilely and/or with olfactory cues; the proximity and color of flags was unimportant. We conclude that despite 18 yr of researchers marking Diamondback Terrapin nests with vinyl flags at this site, Raccoons have not learned to associate flags with nests.

In contrast, we did find some evidence of changes in Raccoon predation behavior which may indicate learning. Our results differed from the Burke et al. (2005) study in two ways: we did not find that ocean water scent (Treatment 8) was associated with high predation rates, and we did not find that human scent (Treatment 7) was associated with low predation rates. Instead, we found that predation rates for artificial nests with high levels of human scent were considerably higher in 2016 than in the previous study, when they were not depredated at all (Burke et al., 2005). This may be because Raccoons have learned to associate some forms of human scent with Diamondback Terrapin nests. Alternatively, Raccoons may have become accustomed or indifferent to human scent, rather than repelled by it as before, and were perhaps attracted to Treatment 7 nests by the tactile cue of soil disturbance (more on this below). These findings suggest that Raccoons can alter their behavior in response to certain olfactory cues over time. Because we had lower sample sizes in this study than did the original, future studies could use larger samples to increase statistical power and confidence in these findings.

Geller (2015) and Buzuleciu et al. (2016) showed that olfactory cues produced by soil microbes, specifically the compound geosmin, are associated with soil disturbance and might be important cues indicating nest locations to predators. We conducted the first tests exploring whether geosmin influenced Raccoon predation on artificial nests. We found that the amounts of geosmin we applied did result in Raccoon predation on artificial nests, but not at levels as high as our standard controls. This suggests the tactile cue associated with soil disturbance may be more important to Raccoons than the olfactory cue associated with soil disturbance. We suggest that further experiments with geosmin are likely to find that it is a valuable addition to studies of nest predation using artificial nests.

Raccoons at RBH switched from consuming only Diamondback Terrapin egg contents without shells early in the nesting season to eating entire eggs with shells later in the season (Burke et al., 2009), so we anticipated a change in their behavior between June and July 2016 in this study as well. Instead, predation rates remained essentially constant over our study so, apparently, Raccoons did not learn to associate or dissociate new cues with Diamondback Terrapin nests over the course of this study.

Across all artificial nest treatments for which we dug cavities (Treatments 1, 2, 3, 4, 5, 7), we observed that most Raccoon digging occurred at the very mid-point between the two marker flags, close to or exactly where we had dug the nest cavity; Raccoons rarely dug elsewhere in the space between the flags. Because we removed visual signs of artificial nests by smoothing the surface sand (mimicking terrapin nesting behavior), this suggests that Raccoons were using nonvisual cues to dig in the particular spot where we dug the nest cavity. These observations corroborate those of Geller (2015), who found that sweeping Ouachita Map Turtle (*Graptemys ouachitensis*) nests with a broom to remove visual surface markings was ineffective in reducing Raccoon predation. Geller (2015) also found that nests with surface markings mimicking those by nesting turtles but lacking cavities were disturbed less frequently than nests with cavities. We conclude that the tactile cue of soil disturbance (the presence of a cavity) is the primary indicator of nest location for Raccoons, not visual cues, moisture, or olfactory cues. Further studies exploring the intersection of tactile and olfactory cues, such as geosmin and latex gloves, would provide greater insights into the relative importance of each type of cue to Raccoons depredating turtle nests.

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