



What Are the Primary Cues Used by Mammalian Predators to Locate Freshwater Turtle Nests? A Critical Review of the Evidence

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Turtle biologists have long been interested in the biotic and abiotic factors that influence the detection of freshwater turtle nests by mammalian predators. Increased knowledge of nest predation dynamics may help develop conservation strategies to increase turtle nesting success by altering or reducing the signal strength of predominant nest location cues. However, despite this long-standing interest, the related research has produced inconsistent and sometimes conflicting results across studies. Here we review much of the existing literature on freshwater turtle nest predation by mammalian predators and attempt to synthesize some general, underlying themes. Available data suggest that raccoons (*Procyon lotor*) primarily use olfactory cues associated with nest cavity construction to locate turtle nests. However, some other predators, including red foxes (*Vulpes vulpes*) and other canids, may commonly use a wider array of cues, including scents from nesting turtles and their eggs as well as visual cues, while foraging. The literature also suggests that the length of the period turtle nests remain vulnerable to nest predation is dependent on the predator community, with raccoons exhibiting relatively short timelines relative to some other predators, including canids. This review has revealed a strong North American bias in published work, highlighting the need for additional studies of turtle nest predation dynamics in other areas of the world where chelonians are often imperiled elements of the biota.

Keywords: Reptilia, Testudines, freshwater turtles, *Procyon lotor*, raccoon, sensory cues, nest predation

INTRODUCTION

For oviparous reptiles, the embryonic stage is one of the most vulnerable phases of the life cycle (Fitch and Fitch, 1967), and high levels of egg predation characterize many chelonian populations (Iverson, 1991). For the majority of turtle species, females provide little or no maternal care, thus successful incubation requires that females select nest sites with appropriate thermal and hydric conditions for incubation (e.g., Schwarzkopf and Brooks, 1987; Wilson, 1998; Morjan, 2003; Pruett et al., 2019) and that nests evade detection by egg predators (Spencer, 2002; Spencer and Thompson, 2003, 2005). Turtle eggs comprise an energy-rich food source (Booth, 2003) and vertebrate egg predators are a predominant source of egg mortality in freshwater turtle species worldwide. Because many turtle species have relatively specific habitat requirements (e.g., Burger and Montevecchi, 1975; Bodie et al., 1996; Wilson, 1998; Paterson et al., 2013) and often exhibit

high levels of nest site fidelity (Freedberg et al., 2005), populations are increasingly vulnerable to elevated nest predation rates as habitat loss and degradation (e.g., vegetational succession) reduces the size of nesting habitat and nest predators such as raccoons (*Procyon lotor*) concentrate their foraging efforts in the remaining areas (e.g., Temple, 1987; Jackson and Walker, 1997; Marchand and Litvaitis, 2004).

Turtle nest predation and the factors that influence it have long been of interest to both amateur natural historians and academics alike. Sensory cues used by predators to identify location of turtle nests are of considerable importance to researchers interested in turtle ecology and conservation, as reduction of the signal strength of these cues may aid management efforts to increase hatchling recruitment. Beginning with possibly the first reference to raccoon depredation of turtle nests/eggs (Kennicott, 1858) and the first experimental efforts to understand the underlying nest location dynamics (Moll and Legler, 1971; Wilhoft et al., 1979), numerous studies spanning nearly 70 years have speculated on, or experimentally evaluated, the sensory cues used by mammalian predators to locate turtle nests. In spite of these efforts, little consensus has emerged as to the primary nest location cues used by mammals, and the related literature is inconsistent and sometimes conflicting; especially perhaps, for raccoons, the most commonly studied turtle nest predator in the world.

The purpose of this review is to provide the first comprehensive synthesis of our present understanding of the sensory cues used by mammalian predators to identify and locate nests of freshwater turtles and to suggest productive areas for future research. In our review, we place an emphasis on predation by raccoons, and often compare findings on other predators to them, because of the disproportionately large number of studies where they were documented to be the predominant nest predator in this cue-focused review (Table 1). Nonetheless, we have included results from studies of other mammalian species where available.

METHODS

Literature Review and Analysis

During the course of this review, we surveyed over 90 papers focusing on or incidentally reporting nest predation metrics for freshwater turtles. We found primary literature by on-line searches using Google, Google Scholar, and the academic research databases of the University of Wisconsin Library System (> 1100 e-collection content selections from Primo Central Index [PCI] from Ex Libris [ProQuest] including Web of Science and Scopus) using the keywords: “turtle:nest:predation”. We also subsequently reviewed the literature-cited sections of all these papers for additional sources relevant to freshwater turtle nest predation. Materials were mostly peer-reviewed, published works, although some unpublished MSc and Ph.D. theses were also included in this review.

For simplicity, we grouped the proposed freshwater turtle nest location cues used by mammalian predators in the

TABLE 1 | Number of papers in this review reporting predominant mammalian predators of natural or artificial nests ($n = 46$ citations).

Nest predator		Number incorporating natural nests	Number incorporating artificial nests
Family	Species		
Procyonidae	<i>Procyon lotor</i>	23	12
Canidae	<i>Canis latrans</i>	1	0
	<i>Cerdocyon thous</i>	0	1
	<i>Lycalopex gymnocercus</i>	0	1
	<i>Nyctereutes procyonoides</i>	1	0
	<i>Vulpes macrotis</i>	1	0
	<i>Vulpes vulpes</i>	6	3
Mephitidae	<i>Mephitis mephitis</i>	5	0
Didelphidae	<i>Dasybus novemcinctus</i>	2	1
Mustelidae	<i>Lontra canadensis</i>	1	1
	<i>Meles meles</i>	2	0
Suidae	<i>Sus scrofa</i>	1	0

reviewed literature into recurring principal types (visual, tactile, olfactory). Within each category we highlight certain studies when, in our view, the presented data are unique or particularly definitive in support of study conclusions or, contrarily, when alternate interpretations appear available for reported results. The provided tables offer an overview of either the claims made or inferences which could be drawn (as in the text, sometimes not stated by the authors) from all reviewed materials. Papers that suggest that certain nest location cues may be operative, but only cite previous publications without providing new data in support, are either not noted or are distinguished as such. Finally, we also made a distinction between nest location cues present soon after nest construction and those present during the hatchling emergence period, and report on these as appropriate. While we recognize that predators likely do not rely exclusively on a single cue, and may use multiple cues to locate turtle nests depending on environmental conditions, our intent is to provide a synthesis of the evidence for the primary sensory cues used by mammalian predators as documented in the literature.

RESULTS

Categories of Proposed Cues

Three broad categories of cues are prominent among those proposed to explain how raccoons and other mammalian predators locate newly created, freshwater turtle nests: (1) olfactory, (2) visual, and (3) tactile. Investigations within each of these categories have attempted to determine the cues of primary importance to nest-foraging predators (Table 2), with varying levels of empirical support—from observation-based speculation to supporting data. Consequently, in some cases, there is disagreement among researchers as to which cues

TABLE 2 | Papers proposing cues used by mammalian predators to locate freshwater turtle nests before the emergence period.

Proposed nest location cue	Nest type	Turtle species	Predominant predator(s)	Citation	Comments
Visual					
Nest itself (via visible soil disturbance)	Artificial (cavities, some with turtle or quail eggs)		<i>Vulpes vulpes</i>	Spencer, 2002	Artificial nests (all with cavities) with more surface disturbance were excavated at higher rates than those with minimal disturbance.
	Artificial (most with cavities, some with turtle scent, all without eggs)		<i>Procyon lotor</i>	Burke et al., 2005	All artificial nests with cavities were smoothed over to resemble natural terrapin nests. Did not resolve the relative importance of visual, olfactory, or tactile components of soil disturbance.
	Artificial (some with cavities without eggs, some with pond water, etc.)		<i>Procyon lotor</i>	Strickland et al., 2010	Surface appearance of artificial nests not described. Did not resolve the relative importance of visual, olfactory, or tactile components of soil disturbance.
	Natural	<i>Chelydra serpentina</i> , <i>Chrysemys picta</i>	<i>Procyon lotor</i>	Wirsing et al., 2012	Did not resolve the relative importance of visual, olfactory, or tactile components of soil disturbance.
	Artificial (cavities with chicken eggs)		<i>Procyon lotor</i>	Holcomb and Carr, 2013	All artificial nests made the same to resemble natural nests. Did not resolve the relative importance of visual, olfactory, or tactile components of soil disturbance.
	Artificial (cavities, some with chicken eggs)		<i>Vulpes vulpes</i>	Dawson et al., 2014	More visual disturbance (subjectively assessed) associated with higher excavation rates.
	Artificial (some with cavities, some with chicken eggs)		Unspecified	Bernstein et al., 2015	Surface appearance of artificial nests not described. Did not resolve the relative importance of visual, olfactory, or tactile components of soil disturbance.
	Artificial (cavities without eggs) and natural	<i>Malaclemys terrapin</i>	<i>Procyon lotor</i>	Czaja et al., 2018	Surface appearance of artificial nests not described. Did not resolve the relative importance of visual, olfactory, or tactile components of soil disturbance.
	Artificial (cavities, some with quail eggs)		<i>Lycalopex gymnocercus</i> , <i>Cerdocyon thous</i>	Perazzo et al., 2018	Surface appearance of artificial nests not described. Did not resolve the relative importance of visual, olfactory, or tactile components of soil disturbance.
Tracks of nesting turtles	Natural	<i>Emydoidea blandingii</i>	<i>Procyon lotor</i> , <i>Vulpes vulpes</i>	Congdon et al., 1983	No supporting data are presented.
	Natural	<i>Chelydra serpentina</i>	<i>Procyon lotor</i> , <i>Vulpes vulpes</i>	Congdon et al., 1987	No supporting data are presented.
	Artificial		Potentially <i>Felis silvestris</i> , <i>Meles meles</i> , <i>Sus scrofa</i> , <i>Vulpes vulpes</i>	Horváth et al., 2021	Camera-based evidence of <i>Felis silvestris</i> and <i>Meles meles</i> following artificial trails made from turtle-scented water to artificial nests.
Olfactory					
Nesting female turtle (incl. fluids and surrogates)	Natural	<i>Trachemys scripta</i>	Unspecified	Cagle, 1950	No supporting data are presented.
	Natural	<i>Chrysemys picta</i>	Unknown, but including <i>Procyon lotor</i>	Legler, 1954	No supporting data are presented.
	Artificial (most with cavities, some with eggs, turtle urine)		<i>Ameiva</i> lizard, <i>Dasyus novemcinctus</i>	Moll and Legler, 1971	<i>Trachemys scripta</i> turtle urine poured on ground (no cavity) was excavated by lizards and armadillos.
	Artificial (most with cavities, some with turtle scent, all without eggs)		<i>Procyon lotor</i>	Burke et al., 2005	Artificial nests with cavities and terrapin-scented sand were excavated at statistically higher rates than those with plain sand in one of two study years.
	Natural	<i>Kinosternon flavescens</i>	<i>Canis latrans</i> , <i>Mephitis mephitis</i>	Tuma, 2006	<i>Canis latrans</i> excavated numerous turtles, including males, from underground burrows in apparent efforts to locate nests. Did not note that soil odor cues may also have been operative.
	Artificial (cavities, some with chicken eggs)		<i>Vulpes vulpes</i>	Dawson et al., 2014	Artificial nests (all with cavities) sprayed with pond water were excavated at higher rates than those without pond water.
	Artificial (some with cavities, some with turtle scent or proxies)		<i>Procyon lotor</i>	Oddie et al., 2015	Artificial nests with <i>Chelydra</i> musk and wetland water (and cavities) were excavated at higher rates than those without applied scents (but no difference when cavity was absent).

(Continued)

TABLE 2 | (Continued)

Proposed nest location cue	Nest type	Turtle species	Predominant predator(s)	Citation	Comments
Turtle eggs (and surrogates)	Artificial (cavities, several treatments)		Potentially <i>Felis silvestris</i> , <i>Meles meles</i> , <i>Sus scrofa</i> , <i>Vulpes vulpes</i>	Horváth et al., 2021	Surmised importance of turtle scent at nests based on camera evidence of scent trail following.
	Natural	<i>Malaclemys terrapin</i>	<i>Procyon lotor</i> , <i>Vulpes vulpes</i>	Burger, 1977	Widespread nest depredation after visible evidence was absent due to wind and rain. Did not resolve the relative importance of olfactory or tactile components of soil disturbance, but suggested olfactory detection of embryonic metabolites or metabolic heat were cues.
	Artificial (cavities, some with turtle or quail eggs)		<i>Vulpes vulpes</i>	Spencer, 2002	Artificial nests (all with cavities) with eggs were excavated at higher rates than those without eggs.
Soil disturbance (general)	Artificial (cavities, some with chicken eggs)		<i>Vulpes vulpes</i>	Dawson et al., 2014	Artificial nests (all with cavities) with eggs were excavated at higher rates than those without eggs.
	Artificial (cavities, some with chicken, quail, or turtle eggs)		<i>Procyon lotor</i>	Wilhoft et al., 1979	Speculated mode relates to soil moisture differences.
	Natural	<i>Emydoidea blandingii</i>	<i>Procyon lotor</i> , <i>Vulpes vulpes</i>	Congdon et al., 1983	Suggested odor of newly created nest was a major nest location cue. No supporting data are presented.
	Artificial (cavities, some with turtle or quail eggs)		<i>Vulpes vulpes</i>	Spencer, 2002	Speculated mode relates to enhancement of turtle and egg scent (possibly also, visual appearance).
	Artificial (most with cavities, some with turtle scent, all without eggs)		<i>Procyon lotor</i>	Burke et al., 2005	Found soil disturbance, perhaps detected visually, to be an important nest location cue, but did not resolve the relative importance of visual, olfactory, or tactile components of soil disturbance.
	Natural	<i>Chelydra serpentina</i> , <i>Chrysemys picta</i>	<i>Procyon lotor</i>	Wirsing et al., 2012	Did not resolve the relative importance of visual, olfactory, or tactile components of soil disturbance. Tested variable was habitat disturbance, not that of nests themselves.
	Artificial (some with cavities, some with chicken eggs)		Unspecified	Bernstein et al., 2015	Found soil disturbance to be a major nest location cue, but did not resolve the relative importance of visual, olfactory, or tactile components of soil disturbance.
Soil disturbance (via moisture differences)	Artificial (some with cavities, all without eggs)		<i>Procyon lotor</i> , <i>Lontra canadensis</i>	Rutherford et al., 2016	Concluded that factors associated with soil disturbance, rather than chemical signals from turtles or their eggs, were nest location cues, but did not resolve the relative importance of visual, olfactory, or tactile components of soil disturbance.
	Artificial (cavities without eggs) and natural	<i>Malaclemys terrapin</i>	<i>Procyon lotor</i>	Czaja et al., 2018	Suggested that rainfall increased nest success by disrupting soil disturbance cues, but did not resolve the relative importance of visual, olfactory, or tactile components of soil disturbance.
	Artificial (cavities, some with quail eggs)		<i>Lycalopex gymnocercus</i> , <i>Cerdocyon thous</i>	Perazzo et al., 2018	Concluded that nest location cues were olfactory and related to cavity construction, but did not resolve the relative importance of visual, olfactory, or tactile components of soil disturbance.
	Artificial (cavities, some with chicken, quail, or turtle eggs)		<i>Procyon lotor</i>	Wilhoft et al., 1979	Proposed soil moisture signal as speculation based on study data. Soil moisture not tested directly.
	Artificial (cavities without eggs) and natural	<i>Graptemys ouachitensis</i>	<i>Procyon lotor</i>	Geller, 2015	Proposed geosmin signal as speculation, not tested directly. Did not resolve the relative importance of tactile components of soil disturbance.
Tactile	Artificial (some with cavities, without eggs, some with turtle scent)		<i>Procyon lotor</i>	Buzuleciu et al., 2016	Proposed geosmin signal as speculation, not tested directly. Did not resolve the relative importance of tactile components of soil disturbance.
	Artificial (some with cavities, some with turtle scent or proxies)		<i>Procyon lotor</i>	Oddie et al., 2015	Claim is tenuous. Did not acknowledge that cavity construction also produces olfactory cues.
	Artificial (some with cavities, some with turtle scent, some with geosmin) and natural		<i>Procyon lotor</i>	Edmunds et al., 2018	Artificial nests with cavities excavated at higher rates than those without cavities. Proposed the use of a tactile sense, although no supporting data are presented for this mechanism, per se.
	Artificial (cavities without eggs) and natural	<i>Malaclemys terrapin</i>	<i>Procyon lotor</i>	Czaja et al., 2018	No supporting data are presented.

TABLE 3 | Papers discounting particular cues used by predators to locate freshwater turtle nests before the emergence period.

Proposed nest location cue	Nest type	Turtle species	Predominant predator(s)	Citation	Comments
Visual					
Nest itself (via visible soil disturbance)	Natural	<i>Malaclemys terrapin</i>	<i>Procyon lotor</i> , <i>Vulpes vulpes</i>	Burger, 1977	Widespread nest depredation after visible evidence was absent due to wind and rain.
	Artificial (cavities, all with quail eggs)		Likely mostly <i>Procyon lotor</i>	Hamilton et al., 2002	3-m of sand placed over artificial nests did not affect depredation rates.
	Artificial (cavities without eggs) and natural	<i>Graptemys ouachitensis</i>	<i>Procyon lotor</i>	Geller, 2015	Depredation rates not affected by eliminating visible nest location sign. Facsimiles of nest markings excavated at low rates relative to artificial nests with cavities.
	Artificial (some with cavities, some with turtle scent or proxies)		<i>Procyon lotor</i>	Oddie et al., 2015	Inconspicuous artificial nests (with cavities) were depredated at high rates. Facsimiles of nest markings excavated at low rates relative to artificial nests with cavities.
	Natural	<i>Chrysemys picta</i>	<i>Procyon lotor</i>	Voves et al., 2016	Human-scored degree of nest crypsis was not a significant predictor of survival.
	Artificial (some with cavities, some with turtle scent, some with geosmin) and natural		<i>Procyon lotor</i>	Edmunds et al., 2018	Smoothed-over artificial nests (with cavities) were depredated at high rates.
Tracks of nesting turtles	Natural	<i>Graptemys ouachitensis</i>	<i>Procyon lotor</i>	Geller, 2012a	Camera data showed non-overlap in turtle and depredating raccoon pathways.
	Artificial (cavities without eggs) and natural	<i>Graptemys ouachitensis</i>	<i>Procyon lotor</i>	Geller, 2015	Eliminating nesting turtle tracks by broom sweeping did not affect depredation rates.
Olfactory					
Nesting female turtle (including fluids and surrogates)	Artificial (cavities, all with quail eggs)		Likely mostly <i>Procyon lotor</i>	Hamilton et al., 2002	Tortoise bladder water applied to artificial nests did not affect predation rates.
	Artificial (cavities without eggs, some with pond water)		<i>Procyon lotor</i>	Strickland et al., 2010	Slough water applied to artificial nests did not affect predation rates.
	Artificial (cavities with chicken eggs)	<i>Macrochelys temminckii</i>	<i>Procyon lotor</i>	Holcomb and Carr, 2013	Excavation rates of artificial nests without female turtle scent cues were similar to natural nests
	Artificial (some with cavities, without eggs, some with turtle scent)		<i>Procyon lotor</i>	Buzuleciu et al., 2016	Excavation rates of artificial nests with female turtle scent cues were not significantly different from those of treatments with neutral or no scent.
	Artificial (some with cavities, all without eggs)		<i>Procyon lotor</i> , <i>Lontra canadensis</i>	Rutherford et al., 2016	Turtle-scented water did not affect excavation rates on artificial nests with cavities. No depredation of treatments using turtle water alone.
	Artificial (some with cavities, some with turtle scent, some with geosmin) and natural		<i>Procyon lotor</i>	Edmunds et al., 2018	Excavation rates of artificial nests without female turtle scent cues were not significantly different from those of treatments with scent or of natural nests.
	Turtle eggs (or surrogates)	Artificial (cavities, some with chicken, quail, or turtle eggs)		<i>Procyon lotor</i>	Wilhoft et al., 1979
Artificial (some with cavities, some with chicken eggs)			not specified	Bernstein et al., 2015	Presence of chicken eggs did not significantly affect depredation rates relative to those without eggs.
Artificial (cavities, some with quail eggs)			<i>Lycalopex gymnocercus</i> , <i>Cerdocoyon thous</i>	Perazzo et al., 2018	Presence of quail eggs did not affect depredation rates relative to those without eggs.
Both turtle scent and eggs (or surrogates)	Artificial (cavities without eggs) and natural	<i>Graptemys ouachitensis</i>	<i>Procyon lotor</i>	Geller, 2015	Excavation rates on artificial nests without eggs or turtle scent cues were similar to those of natural nests.
	Artificial (cavities without eggs) and natural	<i>Malaclemys terrapin</i>	<i>Procyon lotor</i>	Czaja et al., 2018	Excavation rates on artificial nests without eggs or turtle scent cues were similar to those of natural nests.
Soil disturbance (via moisture differences)	Artificial (cavities without eggs) and natural	<i>Graptemys ouachitensis</i>	<i>Procyon lotor</i>	Geller, 2015	Degree of apparent soil moisture did not affect depredation rates on artificial nests.
Soil disturbance (via geosmin signal)	Artificial (some with cavities, some with turtle scent, some with geosmin) and natural		<i>Procyon lotor</i>	Edmunds et al., 2018	Although geosmin was found to be a nest location cue, authors dismissed its relative importance.

have most explanatory value in observed nest predation rates (Tables 2, 3).

Visual Cues

Assessment of Nest-Related Visual Cues

Relatively few studies investigating the sensory cues used by mammalian predators to locate freshwater turtle nests have provided definitive evidence of reliance on visual cues, although most studies to-date have focused largely on just raccoons and study designs sometimes limit interpretations (Table 2). For example, while experimental studies using artificial nests have suggested that nest-surface markings may be important cues for foraging raccoons, uniformity in surface markings among artificial nest treatments (e.g., all smoothed over or all made to resemble natural nest appearance) reduce the ability to test effects of different visual signal strengths or isolate them from other potentially co-occurring cues inherent in artificially constructed nest cavities: a limitation which is only sometimes implied/acknowledged (Burke et al., 2005; Bernstein et al., 2015; Czaja et al., 2018; Perazzo et al., 2018).

Burger (1977) was apparently the first to suggest that visual cues were not necessary for successful nest location by raccoons and red foxes (*Vulpes vulpes*), based on widespread predation of diamondback terrapin (*Malaclemys terrapin*) nests after visual cues had been eliminated on the sand-substrate nesting site by wind and rain. Results of several subsequent studies align with these results, including the experimental evidence provided by Hamilton et al. (2002) who found that 3-m wide areas of sand smoothed over artificial cavities containing quail eggs did not lower excavation rates by raccoons and other predators relative to unobscured nests (see also Edmunds et al., 2018; Table 3). Geller (2015) demonstrated that elimination of surface markings at both natural and artificial nests by broom sweeping did not reduce raccoon depredation rates between experimental and control nests. Additionally, artificial representations of the visual markings made by Ouachita map turtles (*Graptemys ouachitensis*) and snapping turtles (*Chelydra serpentina*) during nesting, but without underlying cavities, were excavated at low rates relative to artificial nests with cavities (≤ 26 vs. 94%, Geller, 2015; ca. 10 vs. ca. 50%, Oddie et al., 2015, from their Figure 3A; respectively). Finally, Voves et al. (2016) found that human evaluation of the degree of visual conspicuousness of natural painted turtle (*Chrysemys picta*) nests was not a consistent predictor of predation likelihood by raccoons.

In contrast, artificial nest cavities simulating surface disturbance by nesting female Australian Murray River turtles (*Emydura macquarii*) were excavated at greater rates by introduced red foxes than control nests with minimal surface disturbance, independent of whether artificial nests contained turtle eggs (80% depredation on disturbed treatment vs. 60% control), *Coturnix* quail eggs (70% disturbed vs. 57% undisturbed), or were without eggs (Spencer, 2002; his Figure 3). Similarly, Dawson et al. (2014) found that red foxes excavated more artificial cavities simulating oblong turtles *Chelodina colliei* nests initially scored as more obvious than those that were more cryptic.

Collectively, we found no papers that suggest visual cues at nests may be important to foraging raccoons provide unambiguous data in support (see Table 2), while several other papers present data to the contrary (Table 3). However, foxes may use visual cues associated with surface disturbance, likely in combination with other signals, to locate turtle nests.

Assessment of Visual/Olfactory Cues From Tracks of Nesting Turtles

Congdon et al. (1983) were the first to suggest that predators may use tracks of nesting females (which contain both visual and olfactory elements) to locate turtle nests. However, their statement was likely based on observation or anecdotal reports. The first experimental test of this hypothesis found that eliminating the tracks of nesting females by daily broom sweeping did not reduce depredation rates by raccoons on either natural or artificial nests (Geller, 2015). Camera data has also demonstrated that the foraging paths of nest depredating raccoons do not align with the paths of nesting *Graptemys* (Geller, 2012a, 2015). Moreover, inducing raccoons to follow scent trails in experimental settings has proved difficult (S. Temple, pers. comm.). While these limited data suggest tracks may not be necessary, *per se*, for raccoons to find turtle nests, it is possible that nesting tracks are followed when more evident, such as in moist soils following rainfall or may be otherwise context dependent at the nest site or geographic location level.

For non-raccoons, however, Horváth et al. (2021), in Slovakia, EU, reported camera-based evidence of trail-following by both European wildcats (*Felis silvestris*) and European badgers (*Meles meles*); both of which followed artificially provided scent trails made of turtle-scented water to artificial European pond turtle (*Emys orbicularis*) nests. To our knowledge, this is the first well-documented report of trail following by a predator of freshwater turtle nests to appear in the literature.

Olfactory Cues

Research on which olfactory cues predators use to identify turtle nests appears early in the literature and continues to be an area of great interest for turtle biologists. In one form or another, olfactory cues have generated most research interest to date (referenced in almost all of the studies in Tables 2, 3). Within the context of nest predation, predators can potentially detect nests directly, using scents produced by nesting turtles, turtle eggs, or disturbed soil profiles produced during nest construction, or indirectly by following scent trails (see above) produced by nesting females during travel to and from nesting sites.

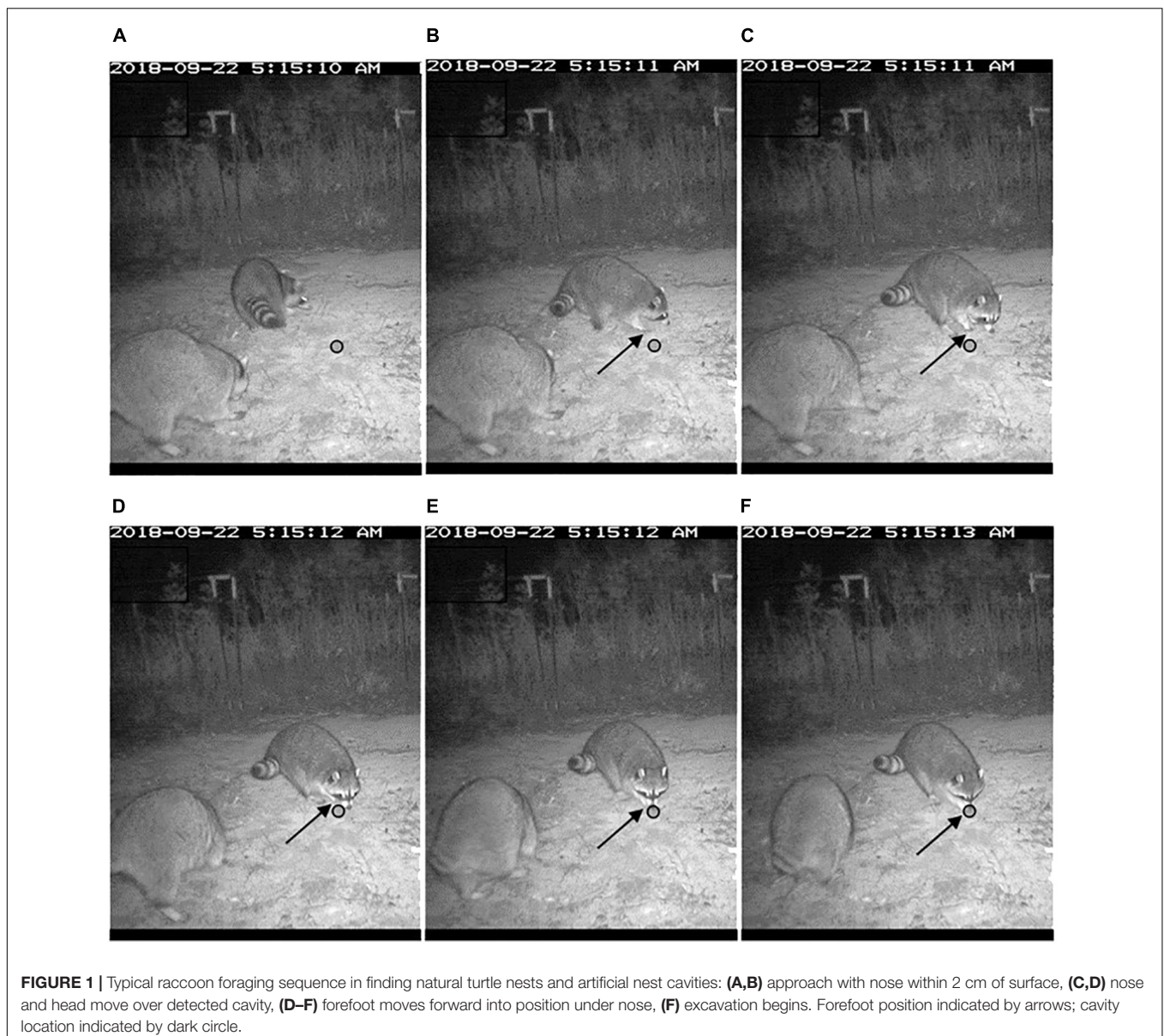
Assessment of Olfactory Cues From Nesting Turtles

In some of the earliest studies addressing the question of turtle nest predation, authors suggested that scents directly associated with oviposition could be used by predators to identify nest location. For example, Cagle (1950) suggested, based on anecdotal reports from professional egg collectors, that scent from gravid female turtle urine or oviductal fluids released during oviposition may function as a nest location cue for predators. Similarly, Legler (1954) speculated that “odoriferous fluid voided by the nesting female” may provide an olfactory cue for predators,

although he did not provide data in support. In a subsequent study, however, Moll and Legler (1971) found that *Ameiva* lizards and armadillos (*Dasyus novemcinctus*) preferentially excavated artificial nests treated with female turtle urine compared to controls. Although that study was based on a small sample size ($n = 1$ treatment replicate), to our knowledge, this is the first experimental study to conclude that some vertebrate predators locate nests using scent cues directly produced by gravid female turtles during oviposition.

Subsequent experimental studies have continued to investigate the relative importance of olfactory cues directly associated with gravid female turtles during nesting. In these studies, authors typically applied water from nearby wetlands or from containers housing captive turtles to artificial nests and measured predation rates (Tables 2, 3). Most of this research has

not provided evidence that scent from nesting female turtles increases the probability of nest predation by raccoons (Table 3). However, Burke et al. (2005) found that raccoons excavated a greater proportion of smoothed-over artificial nests with cavities refilled with *Malaclemys terrapin*-scented sand than when only unscented sand was used (means ca. 93%, $n = 56$ vs. 50%, $n = 56$, respectively; estimated from their Figure 1; difference statistically significant in one of two study years). In a follow-up study (Edmunds et al., 2018), 47% ($n = 17$) of artificial treatments consisting of 100 mL of terrapin-scented sand deposited on the surface were excavated by raccoons, suggesting the use of turtle scent as a cue (not emphasized by authors). However, potentially informative controls of same-source sand without turtle scent were absent, and the excavation rate of artificial nests with cavities with terrapin scent (82.7%, $n = 75$) was similar to that of cavities



without turtle scent (75%, $n = 116$) (2-tailed Fisher's exact test p -value = 0.2831; analysis ours). Similarly, Oddie et al. (2015) found that raccoon excavation rates on their visually inconspicuous artificial nests with cavities supplemented with *Chelydra* musk (ca. 40%) or pond water (ca. 55%) were greater than those without these applied scent cues (ca. 20%; from their Figure 3A). However, locations where these same scents were applied to "artificial nests" that consisted only of visual surface markings were excavated at lower rates (<5% each) than when a cavity was present (overall mean ca. 47%), indicating that some factor associated with nest cavity presence was more influential in nest predation risk than odors directly associated with nesting turtles. Essentially the same conclusion was reached by Oddie et al. (2015), who suggested a synergistic effect of multiple cues in both nest detection and nest predation. However, they considered that cavity-related cue to be tactile, in contrast to some other explanations (such as soil odor, see below).

Related studies on non-raccoon predators are more limited, however Dawson et al. (2014) reported that artificial turtle nests with cavities sprayed with turtle pond water were excavated at higher rates by red foxes than those without pond water, both when they contained chicken eggs (53 vs. 48%) and when chicken eggs were absent (43 vs. 38%). Tuma (2006) noted that coyotes excavated adult yellow mud turtles (*Kinosternon flavescens*), including males, from their underground burrows while searching for nests. He attributed this to coyotes being attracted to the smell of the turtles, rather than to the smell of the eggs, although other cues, such as odors from disturbed soils, may also have been involved. And recently, Horváth et al. (2021) documented scent trail following by two European mesopredators and surmised that odors from nesting *Emys orbicularis* were likely the primary nest location cues.

Overall, although not without exception, most research on raccoons indicates little use of residual turtle scent at nests as nest location cues, while limited evidence suggests that canids and other nest predator taxa may use turtle scent cues to greater extents. More studies on the nest-foraging behaviors of a wider array of mammalian nest predators will be necessary to reveal potential interspecific differences in the reliance on scents associated with gravid female turtles.

Assessment of Olfactory Cues From Turtle Eggs

Artificial nest studies comparing depredation rates of nests with turtle eggs or surrogates to those without eggs provide experimental tests of the importance of egg presence as a factor in nest predation dynamics. In an early study of this type, Wilhoft et al. (1979) found that raccoons actually excavated a greater percentage of the artificial nests depredated in their study ($n = 83$) when they contained only ping-pong balls (41%) than when they contained either turtle eggs (25%) or bird eggs (34%). Similarly, neither the presence nor absence of eggs appeared to influence artificial nest excavation rates in results obtained by Bernstein et al. (2015) in North America (predator species not reported), or by Perazzo et al. (2018) for two native fox species in southern Brazil.

A few raccoon-based studies (Geller, 2015; Oddie et al., 2015; Czaja et al., 2018) have compared concurrent nest depredation

rates between natural nests and artificial nests with cavities lacking both turtle scent cues and eggs (i.e., just refilled cavities). With the exception of Oddie et al. (2015), which found predation rates on natural nests (57% within 4 days of oviposition) to be higher than those of artificial nests without applied scent cues, eggs, or visual disturbance (20%; from their Figure 3A), these studies found that raccoon depredation rates of artificial nests lacking these olfactory signals were similar to those of natural nests, where these potential cues were present.

However, these results contrast with those obtained both by Spencer (2002) and Dawson et al. (2014) for red fox depredation of simulated nests in Australia. Spencer (2002) found higher excavation rates of artificial nests with either turtle or quail eggs than those without eggs, both when surface disturbance was reported as more evident (ca. 80% for turtle eggs and 70% for quail eggs vs. 60 and 45%, respectively) and when efforts were made to minimize disturbance (ca. 60% for turtle eggs and 57% for quail eggs vs. 20 and 15%, respectively; from his Figure 3). Dawson et al. (2014) also reported that artificial nests with chicken eggs were excavated by foxes at higher rates than those without eggs both when sprayed with pond water (53 vs. 43%, respectively) and when not sprayed (48 vs. 38%, respectively).

Overall, there is limited definitive evidence to date suggesting that olfactory cues from nesting turtles or turtle eggs are important cues to raccoons foraging for newly constructed freshwater turtle nests. However, as noted regarding visual cues, olfactory cues from eggs or nesting turtles may be used to a greater extent by nest-foraging red foxes and certain other nest predators (Tables 2, 3).

Tactile and Olfactory Cues From Soil Disturbance

Many researchers have suggested that some factor(s) associated with soils disintegrated during the course of nest construction may function as location cues to freshwater turtle nest predators, with at least 13 of 26 studies reviewed in Tables 2, 3 either suggesting this possibility or providing data demonstrating increased nest predation associated with soil disturbance.

Assessment of Olfactory Cues From Soil Disturbance Versus Tactile Cues

Efforts to resolve which factors associated with soil disturbance function as nest location cues to predators have been complicated by the confounding presence of co-occurring visual, olfactory, and tactile signals inherent in nest cavity construction, resulting in differences in proposed nest detection mechanisms across studies (Table 2). For example, in the earliest experimental demonstration of the role of disturbed soil as a scent cue, Wilhoft et al. (1979) speculated that olfactory differences caused by the variation in soil moisture between disturbed and intact soils were responsible for increased raccoon predation of artificial nests. Alternatively, Spencer (2002) suggested that disturbed soils, in addition to increasing the potential visual evidence, may enhance the odors of nesting females or their eggs. Several studies have reported on predator excavation of artificial nests constructed by removing soil and replacing it into the nest cavity without surrogate eggs or the application of additional olfactory cues

(Tables 2, 3). The elimination of experimental additions of olfactory or visual cues from artificial nests presumably limits predators to two options for locating nests: either olfactory cues originating directly from soil disturbance, or tactile cues resulting from differences in soil density between the nest and the surrounding area.

Geller (2015) and Buzuleciu et al. (2016) attempted to decouple the co-occurring sensory cues present at newly constructed turtle nests, each concluding that the odor of disturbed soils is the primary cue used by raccoons when foraging for turtle nests. In Geller (2015), high predation rates on broom-swept, natural *G. ouachitensis* nests and artificial nest cavities without eggs, showed that neither visual evidence of nesting turtles, nor olfactory cues from nesting turtles or their eggs were necessary for raccoons to locate nests. Although surface hardness differences between natural and artificial nests and the surrounding substrates were not tested, camera data consistently documented raccoons foraging for turtle eggs with noses close to the ground as they searched turtle nesting areas, strongly suggesting a reliance on olfactory, rather than tactile nest cues (Geller, 2015; Figure 1). Based on these observations, scents derived directly from soils disinterred during nest construction were considered primary nest location cues.

Similarly, Buzuleciu et al. (2016) demonstrated that artificial nests with cavities were associated with three to four times higher raccoon predation than those consisting only of surface-applied scent (gravid female *M. terrapin* scent, neutral scent, and no-scent control). This study also tested the hypothesis that scent of recently disinterred soil was the primary olfactory cue used by raccoons to locate terrapin nests by comparing the predation rate of unprotected, recently constructed artificial nests to that of artificial nests “aged” for 48 h within raccoon exclusion cages. They found that depredation rates of newly created artificial nests (all with 10–12 cm deep, refilled cavities) were about five times higher than that for 48-h-old nests (84 vs. 16%, respectively). Caging artificial nests for 48 h presumably allowed volatile organic compounds to dissipate, resulting in reduced olfactory cues for the raccoons. Given that artificial nests were caged for a relatively brief duration (48 h) and no rainfall occurred during the experimental period, it is unlikely that soil compaction in the caged treatments prevented raccoons from using tactile searching to locate the opening of the artificial nest chamber.

Both Geller (2015) and Buzuleciu et al. (2016) independently proposed that geosmin, an odiferous metabolite from the soil microbe *Actinomycetes* aerosolized from disturbed soil profiles and recognized by humans as the smell of disturbed soil (Lindbo et al., 2012), may be one of the underlying olfactory cues produced during nest cavity construction. Based on this proposition, the odor of geosmin alone, or in combination with other related microbial hydrocarbons released by soil disturbance during nest cavity construction, serves as a point-source signal identifying locations of turtle nests to raccoons and possibly other nest predators.

Edmunds et al. (2018), in the first direct test of geosmin as a nest location cue, found that locations where small amounts of geosmin were shallowly injected under soil substrates were, indeed, excavated by raccoons. They further noted that greater

administered volumes of geosmin at the same concentration (0.5 mg geosmin/1 mL methanol) resulted in higher excavation rates (25% excavation rate at 0.1 mL, $n = 20$ vs. 37% at 0.2 mL, $n = 19$). However, because excavation rates of geosmin treatments were lower than those of both natural nests (67%; $n = 42$) and standard artificial nest cavities without eggs (overall 82.7%, $n = 75$, from Treatment 1 in their Table 1), Edmunds et al. (2018) instead concluded that raccoons primarily use tactile cues associated with differences in soil density between nests and surrounding substrates to identify nest locations, although they did not experimentally test anything related to substrate density. Moreover, they did not explore how additional increases in amounts or concentrations of geosmin in their experimental trials may have influenced nest predation rates or discuss how the volatilization timelines of the small amounts of injected geosmin in their study may differ from that within the volumes of soil disturbed during natural nest construction.

The only study purporting to provide data supporting the use of surface hardness as a tactile cue for foraging raccoons is Oddie et al. (2015; Table 2). In that study, artificial nests with manufactured cavities (presenting a less-compacted soil surface relative to the surrounding substrate) experienced a higher depredation frequency compared to artificial nests without cavities, independent of whether visual or additional olfactory cues were present. While Oddie et al. (2015) concluded that raccoons probably use more than one sensory cue to locate nests, they proposed that tactile cues resulting from cavity presence were used to make a final determination as to whether to excavate a nest. However, because all treatment combinations used to test a “tactile” (cavity present) predator response (i.e., applied turtle scent, pond water scent, no-scent, or visual treatment) shared hand-excavated and refilled cavities, their results are confounded by scent cues originating from soil disturbance and therefore make the role of tactile cues difficult, if not impossible, to resolve.

How Long Do Nest Location Cues Last? Assessment of Longevity of Nest Location Cues

With few exceptions, studies indicate that newly constructed turtle nests experience most predation within a few days of construction (Table 4). Nonetheless, a few studies (e.g., Wilhoft et al., 1979) have suggested that the risks of predation on freshwater turtle nests can extend much later into reproductive periods (Table 5). However, one caveat to interpreting the scent cue longevity observations in Wilhoft et al. (1979) is that their raccoon-depredated artificial nests were made in late July, weeks after natural *Chelydra serpentina* nesting activity had ended. Thus, their results only show that raccoons were still foraging at their study sites and would depredate newly constructed artificial nests during these later dates, not that the aging, natural turtle nests made during the just-completed nesting season were still vulnerable to predators. As a result, some authors have used this paper as support for claims of late-season nest cue retention and vulnerability to depredation, without recognizing this important distinction.

Further examination of papers demonstrating long-term nest predation risk reveals two main commonalities which

TABLE 4 | Papers proposing signal strength of cues used by mammalian predators to locate freshwater turtle nests decreases soon after nest construction.

Nest type	Turtle species	Predominant mammalian predator(s)	Citation	Comments
Natural	<i>Chrysemys picta</i>	Unknown, but including <i>Procyon lotor</i>	Legler, 1954	Nest predation rate was at least 5/25 (20%). Most nest depredation within 2 days, often within a few hours.
Natural	<i>Trachemys scripta</i>	<i>Dasybus novemcinctus</i>	Moll and Legler, 1971	Nest predation rate approximated as 78/92 (85%) at one site. Most depredation within 1 or 2 days. Surviving nests relatively free from predation thereafter.
Natural	<i>Graptemys ernsti</i>	<i>Procyon lotor</i>	Shealy, 1976	Multi-year nest predation rate, including avian, approximated as at least 95% based on field observations. Raccoons found nests up to 4 days after construction (as related in Lahanas, 1982).
Natural	<i>Chelydra serpentina</i>	<i>Procyon lotor</i>	Petokas and Alexander, 1980	Known nest predation rate was 17/18 (94%). Most of 40 destroyed nests depredated within 24 h.
Natural	<i>Graptemys ouachitensis</i> , <i>Graptemys pseudogeographica</i>	<i>Procyon lotor</i> , <i>Vulpes vulpes</i> <i>Lontra canadensis</i>	Vogt, 1980	Overall nest predation rate not reported. If a nest not depredated within 2 days, it was usually not disturbed thereafter.
Natural	<i>Chrysemys picta</i>	Not specified	Tinkle et al., 1981	Multi-year nest predation rate was 9/43 (21%). Most depredation within 24 h (67%), then declining. No depredation after 12 days.
Natural	<i>Chrysemys picta</i>	<i>Procyon lotor</i>	Christens and Bider, 1987	Predation rate was 7/16 (43.8%). Of these, 85.7% were depredated within 24 h. The remaining nest was destroyed 32 days after nest construction. No predation after 5 August.
Natural	<i>Emydoidea blandingii</i>	<i>Procyon lotor</i> , <i>Vulpes vulpes</i>	Congdon et al., 1983	Multi-year nest predation rate was 46/73 (63%) before the hatchling emergence period. Of these, 47% were depredated within 24 h and 84% within 5 days. An additional 12% of predation occurred from days 6–30. No predation of remaining 27 nests from day 30 until hatchling emergence period.
Natural	<i>Chelydra serpentina</i>	<i>Procyon lotor</i> , <i>Vulpes vulpes</i>	Congdon et al., 1987	Multi-year nest predation rate was 80/114 (70%) before the hatchling emergence period. Of these, 59% were depredated within 24 h and 73% within 6 days. An additional 20% occurred from days 7 to 18, and 6% from days 19 to 31. No predation of 34 available nests after day 32 or during hatchling emergence.
Natural	<i>Chelydra serpentina</i>	<i>Mephitis mephitis</i>	Robinson and Bider, 1988	Nest predation rate was 113/134 (84%). Of these, 57% were depredated within 3 days. Predation rates declined but ongoing through day 10 with none thereafter.
Natural	<i>Emydoidea blandingii</i>	Unknown, but including <i>Mephitis mephitis</i>	Ross and Anderson, 1990	All 4 nests found intact were depredated within 24 h.
Natural	<i>Pseudemys concinna suwanniensis</i>	<i>Procyon lotor</i>	Jackson and Walker, 1997	Multi-year nest predation rate, including avian, was 114/114 (100%). Of these, 100% were depredated within 2 days. Of 30 other nests protected by screening, 29 had digging within 48 h but waned almost completely after 1 week.
Natural	<i>Malaclemys terrapin</i>	<i>Procyon lotor</i>	Feinberg and Burke, 2003	Nest predation rate was 71/77 (92%). Of 70 depredated nests, 71% were depredated within 24 h and ~89% within 2 days. Longest survival was 7 days, with no depredation thereafter.
Artificial	Mimicking <i>Malaclemys terrapin</i>	<i>Procyon lotor</i>	Burke et al., 2005	Multi-year artificial nest predation rate was 215/448 (48%). Of these, 71% were depredated within 24 h, 81% within 2 days, 94% within 3 days, and 100% within 4 days.
Natural	<i>Emys orbicularis</i>	<i>Meles meles</i> , <i>Nyctereutes procyonoides</i>	Najbar and Szuszkiewicz, 2005	Most nests were depredated 0.5–8 days after construction ($n = 18$).
Natural	<i>Chrysemys picta</i>	<i>Procyon lotor</i>	Rowe et al., 2005	Multi-year nest predation rate was 35/201 (17%). Predation rate on a random subset of nests was 25/122 (20.5%). Of these, 36% were depredated within 24 h, 68% within 2 days. No depredation after 12 days.
Natural	<i>Terrapene carolina</i>	Likely <i>Procyon lotor</i>	Flitz and Mullin, 2006	Nest predation rate was 21/24 (88%). Of these, 86% were depredated within 24 h and all within 3 days.
Natural	<i>Emys orbicularis</i>	<i>Meles meles</i> , <i>Vulpes vulpes</i>	Havaš and Danko, 2009	Almost all nest depredation occurred within 2 days.

(Continued)

TABLE 4 | (Continued)

Nest type	Turtle species	Predominant mammalian predator(s)	Citation	Comments
Natural	<i>Malaclemys terrapin</i>	<i>Procyon lotor</i>	Rahman and Burke, 2010	Nest predation rate was 19/28 (68%). Of these, 100% were depredated within 24 h.
Natural	<i>Graptemys ouachitensis</i>	<i>Procyon lotor</i>	Geller, 2012a	Multi-year nest predation rate was 38/42 (90%). Of 29 nests depredated before the emergence period, 79% were depredated within 24 h, 93% within 2 days. No depredation after 8 days until hatchling emergence period.
Natural	<i>Chelydra serpentina</i> , <i>Chrysemys picta</i>	<i>Procyon lotor</i>	Wirsing et al., 2012	Multi-year nest predation rate was 54/94 (57%) for <i>Chrysemys picta</i> and 166/198 (84%) for <i>Chelydra serpentina</i> . Most predation within 24 h (74% for <i>Chrysemys</i> , 82% for <i>Chelydra</i>). In total, 98% depredation occurred within 5 days (both species combined).
Artificial	Mimicking <i>Macrochelys temminckii</i>	<i>Procyon lotor</i>	Holcomb and Carr, 2013	Multi-year artificial nest predation rate was 90/90 (100%). Of these, 86% were depredated within 24 h, 94% within 2 days. Last depredated nest was ca. 5 days old.
Artificial	Mimicking <i>Terrapene ornata</i>	Not specified	Bernstein et al., 2015	Typically, any treatment with disturbed soil was depredated within 2–3 days. Also noted that natural nests were almost never depredated after 2 weeks.
Natural and artificial	<i>Graptemys ouachitensis</i>	<i>Procyon lotor</i>	Geller, 2015	Multi-year natural nest predation rate was 35/36 (97%). Of these, 35/35 (100%) were depredated within 24 h. In total, 32 of 33 artificial nests excavated within 24 h, 1 within 2 days.
Natural	<i>Chelydra serpentina</i>	<i>Procyon lotor</i>	Oddie et al., 2015	36 of 63 (57%) nests were depredated within 4 days (not monitored thereafter).
Natural	<i>Emydoidea blandingii</i>	not specified	Byer et al., 2018	Modeled and actual nest depredation probabilities were low for nests that survived the first few days after construction.
Natural	<i>Glyptemys insculpta</i>	<i>Procyon lotor</i> , <i>mephitis mephitis</i>	Bougie et al., 2020	29 of 45 (64%) depredated nests were destroyed within 5 days.

may explain divergence from studies that report shorter nest vulnerability timelines: the inclusion of data from hatchling emergence periods in predation risk assessments or having nesting areas with more diverse predator communities, rather than just raccoons (Table 5). Both of these factors have introduced complexity, as well as some confusion, into the literature on turtle nest predation dynamics, and are discussed below.

Evidence for Renewed Nest Location Cues During Hatchling Emergence Periods

Beginning with Burger (1977), many authors have suggested that new nest location cues arise at the onset of, or during, the hatching period as hatchlings fracture eggshells and absorb residual yolk sacs, yet remain in or above the nest chamber prior to emergence. In studies surveying entire reproductive periods, these renewed cues result in a secondary nest predation peak and extend the reported age of depredated nests relative to studies with shorter timelines. Pre-emergence cues of nest location may include olfactory signals from embryonic fluids and disturbed soils created by subterranean hatchling movements, or hatchling vocalizations (Ferrara et al., 2012; Riley and Litzgus, 2014; Geller and Casper, 2019). Upon surface emergence, new nest location cues potentially include odors arising from nest cavities via exit holes (Congdon et al., 1983; Christens and Bider, 1987), and visual cues provided by hatchling tracks (Congdon et al., 1983;

S. D. Gillingwater, *pers. comm.*, in Riley and Litzgus, 2014). However, the importance of potentially confounding, olfactory cues co-occurring with visible tracks has not been investigated, nor have any published studies attempted to resolve the relative importance of these possible cues on predation frequency during the hatchling emergence period.

Assessment of Differences Among Predator Species in Nest Detection Timelines

A less often recognized source of variance in reported nest survival timelines concerns the composition of the involved predator community. To date, Galois (1996) represents the only experimental work that has attempted to directly assess the differential sensory capabilities of common turtle nest predators, finding that olfactory cues likely play a predominant role in turtle nest detection by both striped skunks (*Mephitis mephitis*) and raccoons, based on food-conditioning and discrimination learning trials. Galois (1996) further determined that striped skunks are likely more narrowly reliant on olfaction than raccoons, in accord with previous research demonstrating the importance of olfaction to foraging skunks (Langley, 1979; Nams, 1991). Raccoons, though also characterized by a well-developed olfactory sense, were found to use both tactile and visual cues to a greater degree than skunks.

Some inferences regarding the role of differential olfactory sense development on nest depredation dynamics in field settings

TABLE 5 | Papers suggesting the signal strength of cues used by mammalian predators to locate freshwater turtle remains long after nest construction.

Nest type	Turtle species	Predominant mammalian predator(s)	Citation	Presented data	Comments
Natural	<i>Malaclemys terrapin</i>	<i>Procyon lotor</i> , <i>Vulpes vulpes</i>	Burger, 1977	Predation rate was 20% of extant nests during first 30 days period, 27% during 30–60 days, and 75% during 60–90 days.	60–90 day period included emergence period (mean emergence = 72 days). Nests were hand-excavated when ≥ 65 days old, possibly affecting nest location signals (however, see Burger, 1977, p. 460).
Artificial		<i>Procyon lotor</i>	Wilhoft et al., 1979	Artificial nests made in July (various types) were depredated at moderate rates (12–40%) in late July-early August, several weeks after nesting season had ended in early June.	Depredated artificial nests were newly created. Thus, data do not relate to depredation risk of aging natural or artificial nests.
Natural	<i>Graptemys ouachitensis</i> , <i>Graptemys pseudogeographica</i>	<i>Procyon lotor</i> , <i>Vulpes vulpes</i> , <i>Lontra canadensis</i>	Vogt, 1980	<i>Lontra canadensis</i> depredated nests during June, July, and August.	Hatchling emergence began in August.
Natural	<i>Chrysemys picta</i>	<i>Mephitis mephitis</i>	Snow, 1982	Most nests depredated on the day of construction (9 of 33), but depredation continued through day 22.	23 of 39 predation events were by skunks, 5 by chipmunks (<i>Tamias striatus</i>), and only 4 each by foxes and raccoons. Oldest nest destroyed by skunks was 22 days old, for foxes was 8 days old, for raccoons was probably ≤ 5 days old (from Figures 2, 3).
Natural	<i>Glyptemys insculpta</i>	Unspecified	Brooks et al., 1992	All of 17 depredated nests were destroyed during a single week, around 9 weeks after the last nest was constructed.	Nine-week nest predation date may be at the beginning of the hatching or emergence period.
Natural	<i>Emydoidea blandingii</i>	Likely <i>Procyon lotor</i>	Standing et al., 1999	Reported evidence of fresh predation during late August and early September.	Noted increases in predator activity in the autumn after a mid-nesting season lull. Hatchling emergence began in early September or October.
Natural	<i>Gopherus agassizii</i>	<i>Vulpes macrotis</i>	Bjurlin and Bissonette, 2004	In one study year, 1 of 8 nests was depredated within 1 week of oviposition, whereas the rest were depredated during early August, more than one month after nest construction.	Nests were protected from depredation after 70 days. Authors suggested nest visitation rates may have affected predation rates.
Natural	<i>Malaclemys terrapin</i>	<i>Procyon lotor</i> , <i>Dasyopus novemcinctus</i>	Butler et al., 2004	Overall nest predation rate was 197/310 (63.5%). Most nest predation within 24 h (74.3% in 1997, $n = 144$ and 53.9%, $n = 166$ in 2000). Older nests were less likely to be depredated, however some (12.1%) nests were depredated 3–53 days, or longer, after construction.	Nests depredated at ages 54–106 days ($n = 26$) were during the emergence period.
Natural	<i>Graptemys oculifera</i>	<i>Dasyopus novemcinctus</i> , <i>Procyon lotor</i>	Jones, 2006	86% ($n = 118$) of caged nests were attacked by predators as late as 69 days after nest construction. Over 42% were within the first 24 hrs and 81% within the first 14 days.	Late-season disturbance at caged nests may relate to hatchling emergence activity, as means were 64.4 ± 4.7 days to pipping, 76.3 ± 7.7 days to emergence itself, and 12.0 ± 5.5 days between pipping and emergence.
Natural	<i>Malaclemys terrapin</i>	<i>Procyon lotor</i>	Rahman and Burke, 2010	In one set of experiments, 9/11 (82%) of nests protected, then unprotected, after 21–25 days were depredated up to 11 days later.	Researcher removal of nest cages may have produced new nest location cues, possibly via stake removal or efforts to visually conceal the location.
Artificial		<i>Vulpes vulpes</i>	Dawson et al., 2014	Four types of artificial nests, including some with just refilled cavities, were excavated throughout entire 60-d monitoring periods.	46% of 580 initial artificial nests excavated within 2 months of construction, mostly within 30 d.
Natural	<i>Chelydra serpentina</i> , <i>Chrysemys picta</i>	<i>Vulpes vulpes</i> , fewer <i>Procyon lotor</i>	Riley and Litzgus, 2014	In total, 17% of snapping turtle and 14% of painted turtle nest predation was in first week. Another peak occurred from weeks 10 to 14 and up to 105 days after nest construction for snapping turtles and during weeks 3–4 and 11–12 for painted turtles and up to 109 days after nest construction.	Part of the late period depredation events for both species are just before, and continuing into, hatchling emergence periods (e.g., their Figure 3). Canid predator presence increased later in incubation periods.

can perhaps be gained by comparing depredation timelines in studies of both natural and artificial turtle nests. For example, in Snow (1982), often cited in support of long nest vulnerability timelines, striped skunks were strongly predominant predators, with little on-site presence by raccoons. Although that study did not examine nor discuss the potential implications of differential sensory capabilities among predator species, it is possible to deduce from Figures 2, 3 in that study that the oldest nests destroyed by skunks and foxes were 22 days old and 8 days old, respectively, while the oldest nest depredated by raccoons was likely ≤ 5 days old. Similarly, Congdon et al. (1987), proposing a differential, olfactory basis, found that red foxes destroyed older *Chelydra serpentina* nests than did raccoons (mean = 9.4 days, $n = 32$ vs. mean = 1.9 days, $n = 13$, respectively). Dawson et al. (2014) also documented long predation timelines by red foxes, with ongoing excavation of artificial nests up to 60 d old occurring throughout monitoring periods. The mid-season nest predation exhibited by skunks and canids likely reflects reliance on turtle egg scent cues themselves, as these odors are presumably the only ones remaining after potential visual, tactile, and other olfactory cues have faded.

In a recent review of nest predation timelines, Riley and Litzgus (2014) presented age-related nest predation data both from their own as well as previously published research. They concluded that nest location cues persist during the several-week period following nest construction and suggested that additional nest predation peaks after week one for the turtle nests in their study were associated with increased numbers of canids at these later dates. They also noted that interspecific differences in cues used by predators, in addition to predator densities and individual behavioral differences, may be partially responsible for reported variation in nest predation timelines. However, while Riley and Litzgus (2014) thus noted the potential for a predator species effect on nest depredation timelines, they did not discuss how differential sensory capabilities among predator species, *per se*, may have impacted their findings or largely explain the results of other research [e.g., the long vs. short predation risk timelines of Snow (1982) and Burke et al. (2005), respectively; see their Table 1]. In fact, red foxes, able to detect and depredate relatively old nests (see above), were strongly predominant in their study and may have been responsible for the somewhat atypical nest predation patterns they observed.

Available evidence thus indicates that the age-related risk of predation is, at least in part, dependent on the species composition of the local predator community due to differential sensory abilities among species.

DISCUSSION

In this review we have attempted to synthesize much of the literature regarding the cues used by mammals in the predation of turtle nests derived from observational and experimental research produced over the past several decades. The bulk of the empirical data from predation studies on both natural and artificial nests suggests that raccoons, the predator most often the subject of such studies, predominantly rely on scent cues of

disturbed soils to locate recently constructed freshwater turtle nests. Predation rates of natural nests remain high even after all potential visual cues (i.e., sign of nests and nesting turtle tracks) have been experimentally eliminated, and artificial nests with manufactured cavities are consistently found and excavated by raccoons at higher rates relative to those without cavities, regardless of whether or not they contain turtle scent, egg scent, or visual surface markings. In this regard, suggestions that female turtles make purposeful attempts to visually conceal nest locations by carefully finessing the nesting substrate (sensu Strickland et al., 2010) are, thus, called into question as far as raccoon predation is concerned. However, reducing the visual cues to nest presence is likely important in reducing predation risk by avian predators, whose foraging for turtle nests appears to be primarily visually based (e.g., Burger, 1977; Jackson and Walker, 1997; Butler et al., 2004; see also Voves et al., 2016). In contrast, foxes and other canids, striped skunks, and other predators may not only have better-developed olfactory senses than raccoons, but may also more commonly use a greater number of nest location signals in addition to those from recently disturbed soils, including visual surface disturbances and odors of nesting turtles and their eggs, to locate nests.

Raccoons are particularly effective nest predators because they have the capacity to respond to seasonal changes in food supply (Daglish and Anderson, 1979) and concentrate foraging effort at turtle nesting areas when these new food resources become available (Petokas and Alexander, 1980; Geller, 2012a). Raccoons are naturally inquisitive, and it is likely that they investigate a variety of scents suggestive of food. Typically, when turtle nests are located in soil or sand substrates, both egg and soil odors co-occur in newly constructed nests. Although it is possible that odors from disturbed soils may initially present a stronger olfactory signal than that from buried eggs, raccoons may still be able to resolve the egg-related odors within the olfactory mix, at least when nests are only a few days old. Nonetheless, raccoons appear to use the scent cue produced by disinterred soil as a “default” cue to indicate the presence of turtle eggs or perhaps other food items. Cueing in on olfactory signals of soil disruption would be an efficient foraging strategy because many potential prey items below the substrate may produce these same environmental signs, therefore reducing or eliminating the need for prey-specific scent recognition or detection.

In contrast, reliance on tactile cues to initially locate freshwater turtle nests would seem unlikely from an efficiency perspective, as it is reasonable to assume that raccoons, like other predators, use a foraging strategy that optimizes energetic gain while minimizing expenditure of energy and time (Emlen, 1966). Given the lack of unambiguous data in support of tactile searching by nest-foraging raccoons, and the likely inefficiency of physically detecting point sources of varying surface hardness over large nesting areas compared to “distance” senses of olfaction or vision (Galois, 1996), available evidence suggests that tactile searching is, at best, a complimentary, rather than primary means of locating turtle nests.

Survival of turtle nests is not only a function of nest cue signal strength, but also of predator species, the timing of predator presence after nest construction, and predator proximity to

nests. Relatively short nest survival intervals, typically within 2 or 3 days, appear nearly universal where raccoons are the predominant predator (**Table 4**), while at least some nests that initially survive short-term predation are depredated at later dates when the mammalian predator community is more diverse and includes, for example, canids (**Table 5**). Canids, have long been known to possess advanced olfactory senses (Green et al., 2012; Lea and Osthaus, 2018). Although comparative behavioral studies between canids and other carnivores are scarce, at least some canids have large olfactory turbinal surface areas relative to most other carnivores that have been examined (reviewed in Lea and Osthaus, 2018) and red foxes have exceptionally large olfactory turbinal surface areas for their size (Green et al., 2012). We thus suggest that generalized claims as to nest predation risk extending well into nesting seasons be interpreted cautiously, as these timelines appear dependent, at least in part, on the composition of the local predator community. In areas where raccoon predation is dominant, nests may be most at risk shortly after oviposition and then again during hatching and emergence. In contrast, in environments where canids, for example, are dominant, the predation window may extend from oviposition through hatching due to their exceptional olfactory sensitivities.

While this review has allowed us to make generalized statements regarding the primary cues used by predators, the potential for local or context-dependent variation in nest predation dynamics must also be recognized. For example, some individual raccoons or populations may habitually follow the tracks of nesting female turtles to find nests, particularly when tracks are most evident in sparsely vegetated, moist substrates (e.g., see pg. 26 in Buhlmann et al., 2008). Similarly, the occasional excavation of artificially made markings that mimic those of natural nests (Geller, 2015; Oddie et al., 2015), suggests some use of visual cues in locating nests, as does the direct sighting of in-process, nesting turtles themselves (e.g., Jackson and Walker, 1997). Nesting sites also vary in surface soil hardness (e.g., sandy vs. organic soils), influencing the potential for tactile nest detection among sites (Oddie et al., 2015). Thus, while the well-established importance of olfaction to raccoon foraging (Bowman and Harris, 1980; Ruzicka and Conover, 2011) aligns with the primary findings of this review, some variation in cues and sensory modes used to locate nests is to be expected given possible differences in the relative strengths of nest location signals among settings and the wide array of well-developed senses available to these and other turtle nest predators.

Based on the results of this review, we have identified areas of nest predation dynamics in need of further study. We support Edmunds et al. (2018) in calling for more research on the role of geosmin—and possibly other volatile soil hydrocarbons—in turtle nest detection, particularly as it may be a common factor underlying mammalian detection of natural nest cavities globally. More generally, this review has revealed a significant need for expanded research on turtle predation dynamics in areas outside of North America (85.7% of the 49 citations in **Tables 2–5** originate from the United States and Canada). In addition to expanding our knowledge of similarities and differences among mammalian taxa regarding sensory cues used to identify turtle nests, a broader overview of species-specific

mammalian nest predation dynamics may help inform local conservation strategies as to which predator species are in greatest need of management and when nest protection measures are most effectively applied. In these efforts, we anticipate that the increasing use of trail cameras will likely lead to larger and better-resolved datasets regarding turtle nest survival timelines and nest predators in both natural and experimental settings. Multi-year studies on both specific turtle populations and across geographies will be particularly useful in understanding how nest predation dynamics may change over space and time (Edmunds et al., 2018) as a result of individual predator variation or culturally influenced learning (e.g., for raccoons, Gehrt, 2004).

Regardless of the potential for targeted management to reduce turtle nest predation by disrupting nest location cues (e.g., by shallow-tilling substrates to obscure the olfactory signals of newly constructed nests), maintaining or optimizing nesting area integrity in terms of vegetative cover, soil condition, and other ecological characteristics over long periods of time remains paramount. In addition to predator exclusion (Buhlmann and Osborn, 2011; Geller, 2012b; Quinn et al., 2015), efforts to increase turtle nesting success where raccoons are the predominant nest predator may benefit from enlarging and maintaining the open habitats often used by nesting turtles, thereby minimizing chance encounters with the point sources of disturbed soils identified as predominant nest location cue for raccoons (see Temple, 1987; Jackson and Walker, 1997; Marchand and Litvaitis, 2004; Vilardell et al., 2008). However, even with such efforts, success may be limited in areas where raccoons have substantially elevated populations due to anthropogenic influence or where foxes are important nest predators, as they, and possibly some other nest predators, may also use scent trails and other cues to individually track and locate nests over greater distances in a more directed fashion.

One of the few ways turtles may be able to reduce the olfactory and visual cues that necessarily arise during nest cavity construction is to nest shortly before significant rainfall. However, to date, there is little evidence that turtles show this propensity (e.g., see Czaja et al., 2018). Total annual precipitation and single event precipitation amounts are expected to increase worldwide under present and projected climate change scenarios, although these effects will not be evenly distributed (Wuebbles et al., 2017). In areas likely to experience increased precipitation frequency and amounts (e.g., northeastern United States) nest success may increase due to greater proportions of nests being constructed before rainfall by chance alone, while the opposite may be true in areas likely to experience historically lower levels of precipitation (e.g., Mediterranean Basin) (see also Czaja et al., 2018). However, as changing rainfall patterns also impact air and substrate temperatures, nest site flooding potentials, and the amount and composition of vegetational cover on nesting areas—all of which have implications for nesting habitat suitability and embryo/hatchling survival—the ultimate impact of anthropogenic precipitation change on worldwide turtle populations is unclear and will likely be context dependent.

AUTHOR CONTRIBUTIONS

GG conducted the literature review and wrote the first draft including 4 of the 5 tables and the figure. SP edited and contributed to the first and subsequent drafts, provided additional citations, and contributed to 1 of 5 tables. Both authors contributed to the article and approved the submitted version.

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