BRILL

Predator and duck behaviours at depredated nests in wetlands of Great Salt Lake, Utah

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Abstract

Nest depredation is one of the greatest threats posed to ground-nesting ducks. We employed cameras to monitor 164 duck nests (71 cinnamon teal, *Spatula cyanoptera*, 44 gadwall, *Mareca strepera*, 38 mallard, *Anas platyrhynchos*, and 11 nests of unknown species) in the wetlands surrounding Great Salt Lake, from 2015–2021. Of the 164 nests, 21% were successful, 73% were depredated and 7% were abandoned. We observed predators at 99 of the 119 depredated nests; predators at 20 nests went undetected. Raccoons (*Procyon lotor*, $N = 44$ depredated nests) and striped skunks (*Mephitis mephitis*, $N = 43$) were the most common of the 99 nest predators recorded. Other predators that depredated nests included long-tailed weasels (*Mustela frenata*), northern harriers (*Circus hudsonius*), California gulls (*Larus californicus*), Sandhill cranes (*Antigone canadensis*), common ravens (*Corvus corax*), coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*). Neither the number of eggs removed per depredation event nor the number of eggs remaining varied by predator species. Depredated nests were easier for predators to find than undisturbed, incubated nests, resulting in 68% of depredated nests being visited by multiple predators. All hens detected the approach of a predator and flushed before the predator reached the nest; no hens attempted to defend their nest or attack the predator. Only 21% of hens returned to their depredated nest, and those that did remained off their nest an average of 33 h and 23 h after their nest was depredated by a raccoon or skunk, respectively. Seventeen percent of hens resumed incubation of their depredated nest, but only 1 nest to which a hen returned successfully hatched an egg. Depredation events of raccoons and skunks were not distributed randomly during the 24-hour day, but rather occurred most often during the night and nautical twilight, and rarely during the day. Depredation events of avian predators occurred during the day, rarely during twilight, and none during the night. Depredation events during the night were more likely when the wind was calm but temperature, humidity, and actual moon illumination had no impact. Depredation events by

skunks and raccoons occurred more often during the 1st and 4th phases of the moon (new moon) than in the 2nd or 3rd phase.

1. Introduction

Nest depredation is the greatest threat to the success of ground-nesting duck nests (Klett et al., 1988; Sargeant & Raveling, 1992; Sargent et al., 1998; Walker et al., 2005). In the wetlands of Great Salt Lake (GSL), striped skunks (*Mephitis mephitis*) have historically been present. However, red foxes (*Vulpes vulpes*) and raccoons (*Procyon lotor*) have arrived only in the last few decades (West, 2002; Frey & Conover, 2006). After the arrival of these new predators, few waterfowl nests were successful (West, 2002). These wetlands were once known to produce hundreds of thousands of ducks (Bellrose, 1980) but now produce a fraction of that (Baldassarre, 2014).

Knowing which predators threaten nests, and how to reduce their impact on nests has been of great interest to waterfowl managers (Klett et al., 1988; Crabtree et al., 1989; Sargeant & Raveling, 1992; McKinnon & Duncan, 1999; Ringelman et al., 2014). In recent decades, researchers have followed the method for identifying nest predators developed at the Northern Prairie Science Center (Sargeant et al., 1998). Using this method, researchers and managers examine the remains of eggshells and the condition of a nest to determine which predator depredated the nest. This method for predator identification is unreliable due to the overlap in appearance of the remains of eggs, shells, and nesting material left by different predators; the complete removal of eggs from a nest leaving no visual signs; multiple visits from different predators before scientists get to inspect the nest; partial depredation of nests; and parental activity (e.g., removal of broken eggshells) at nests (Lariviere, 1999). Nest cameras have created the opportunity to identify predators more accurately and investigate questions about the behaviour of predators and prey during and after a predator depredates a duck nest (hereafter referred to as a depredation event). Partially depredated nests can still contribute to overall nest success rates and to duckling production if hens return to their nests to resume incubating any remaining eggs (Croston et al., 2018). Accounting for partial clutch success can be an important aspect of

estimating the correct nesting success rate and its impact on duckling production (Ackerman et al., 2003).

While much has been learned about the severity of the problem, we know little about the behaviour of predators during and after depredation events. Predators locate nests using various senses and search methods. The most common modalities used by predators to locate ground-nesting birds are vision and olfaction (Conover, 2007; Fogarty et al., 2017). Visual predators typically are avian species that hunt during the day, flying above nesting habitats or hunting from elevated perches.

Being small-bodied, duck hens do not have the ability to defend themselves or their nest physically against predators as some geese (*Branta* spp.) and swans (*Cygnus* spp.) do (Thompson & Raveling, 1987; Hawkins, 1987). Although hens were observed to defend their nests against some avian predators (Jahren, 2012), it was speculated that this was likely due to the low danger that these predators posed to the hens themselves. However, hens can defend their nests from predators through indirect methods such as selecting a nest site that is concealed from predators (Bell, 2022).

Olfactory predators use olfaction to locate prey and hunt primarily at night. These predators have a heightened sense of smell, allowing them to detect odorants emitted by prey animals (Conover, 2007). Odorants emitted from an animal, or its nest, create an odour plume (Conover, 2007; Borgo & Conover, 2016). Olfactory predators, such as raccoons and striped skunks, are common threats to ground-nesting birds (Klett & Johnson, 1982; Cowardin et al., 1985; Ringelman et al., 2014; Croston et al., 2018).

Olfactory predators may prefer to hunt when weather favours the use of olfaction; these conditions include low temperatures, slow winds (Conover, 2007; Web et al., 2012; Borgo & Conover, 2016), high humidity (Conover, 2007), or wet surfaces from dew or rain (Pleasant et al., 2003). Olfactory predators can hunt regardless of light levels and may not need moonlight to detect prey (Soria-Diaz et al., 2016; Pratas-Santiago et al., 2017). If a predator is solely hunting for duck nests, moon phase does not matter, but predators are probably searching for other prey and find duck nests incidentally during these searches (Cowardin et al., 1983). Thus, we would expect these predators to be more active around the new moon or when illumination from moonlight is minimal because prey that rely upon vision to detect approaching predators would be more vulnerable when night skies are dark. For prey that can retreat to sanctuaries where they are safe from predators,

such as rodents that have burrows, the prey would be most vulnerable to predators when they leave their sanctuaries to forage. Consequently, predators would be expected to hunt these prey while they are foraging (Penteriani et al., 2013). If foraging activities of rodents or other prey are influenced by the lunar cycle, then the foraging patterns of their predators may follow a similar pattern. For example, lynx (*Lynx pardinus*) activity during the lunar cycle is tied to the activity of rabbit (*Oryctolagus cuniculus*; Penteriani et al., 2013).

Behaviours of predators and hens at nests is relatively unstudied in dabbling ducks (Croston et al., 2018). In this study, we seek to answer the following questions: How long does a predator spend at a nest during a depredation event, how many eggs does it consume or destroy per event, how many eggs are left unharmed, are depredated nests found faster by subsequent predators than nests that have not yet been depredated, and do predators visit a nest that has already been depredated once? We hypothesized that a predator would spend little time at a nest and that it would eat the entire clutch. We also hypothesized that predators would find previously depredated nests faster than nests that had not yet been depredated because a predator might return to a nest it depredated previously to make sure that the hen did not lay more eggs after the depredation event and that nothing edible remained at the nest site, or because the smell of broken eggs may attract other predators to the nest (Holopainen, 2020).

We also ask, how often does a hen return to the nest after a depredation event, how long do hens stay away from their nest before returning, and do hens resume incubating a partially depredated nest? We hypothesized that a hen would return to its nest to check for surviving eggs because the hen would want to continue incubating any remaining eggs, but that it would wait for a few hours after a depredation event to make sure the predator had left. We also hypothesized that a hen would be more likely to incubate its depredated nest if several eggs survived the depredation event because its direct fitness would be higher if more eggs hatched than if only a few eggs hatched.

Finally, we ask if the weather and light conditions on a given night affect whether nests are depredated, and if depredations follow a lunar pattern. We hypothesized that depredation events would occur more frequently when temperatures are low, winds mild, humidity high, and that depredation events are more likely during nights when the skies were dark (Conover, 2007). We

also hypothesized that depredations would occur around the new moon when the moon provides little light.

2. Materials and methods

2.1. Study area

We located nests in the wetlands bordering GSL, Utah, USA from 2015–2021 (Figure 1). Utah Division of Wildlife Resources managed several waterfowl management areas (WMAs), which provided habitat for thousands of ducks during the spring, summer and autumn. We located and monitored nests at Salt Creek WMA, Public Shooting Grounds WMA, Ogden Bay WMA, and Farmington Bay WMA. Nests were also monitored at the U.S. Bear River Migratory Bird Refuge (hereafter BRMBR), managed by the U.S. Fish and Wildlife Service and the Bear River Duck Club. All were built to impound freshwater flowing down river towards GSL to make shallow impoundments for waterfowl and waterbird use. Dams creating the impoundments averaged a height of 1 m above the water and were 15–20 m wide with a dirt road running along the centre. Impoundments usually occurred adjacent to each other as they caught water flowing down the river. The impoundments filled as spring runoff flowed towards GSL. The dams were often the only dry land in the marshes during wet springs. Dams were constructed so that both of their sides had a gentle slope from the water's edge up to the road. Dams were covered with grass and forbs, which provided nesting habitat for ducks, other waterfowl, and waterbirds. Trees did not occur on the dams or in our study area so there were few avian predators that hunt from perches or nest in trees, including common ravens (*Corvus corax*), American crows (*Corvus brachyrhynchos*), black-billed magpies (*Pica hudsonia*) and red-tailed hawks (*Buteo jamaicensis*). More common were northern harriers (*Circus hudsonius*). Thousands of California gulls (*Larus californicus*) nest in several colonies in BRMBR but not in the WMAs. Winters in northern Utah are so long and summers so short that few snakes in GSL marshes grow large enough to swallow a duck egg.

Three duck species nested on the dikes, cinnamon teal (*Spatula cyanoptera*), mallard (*Anas platyrhynchos*) and gadwall (*Mareca strepera*). Each of the management areas are near farmland and residential areas, both of which supplement the raccoon and skunk populations, providing a source for many of the predators present in these areas.
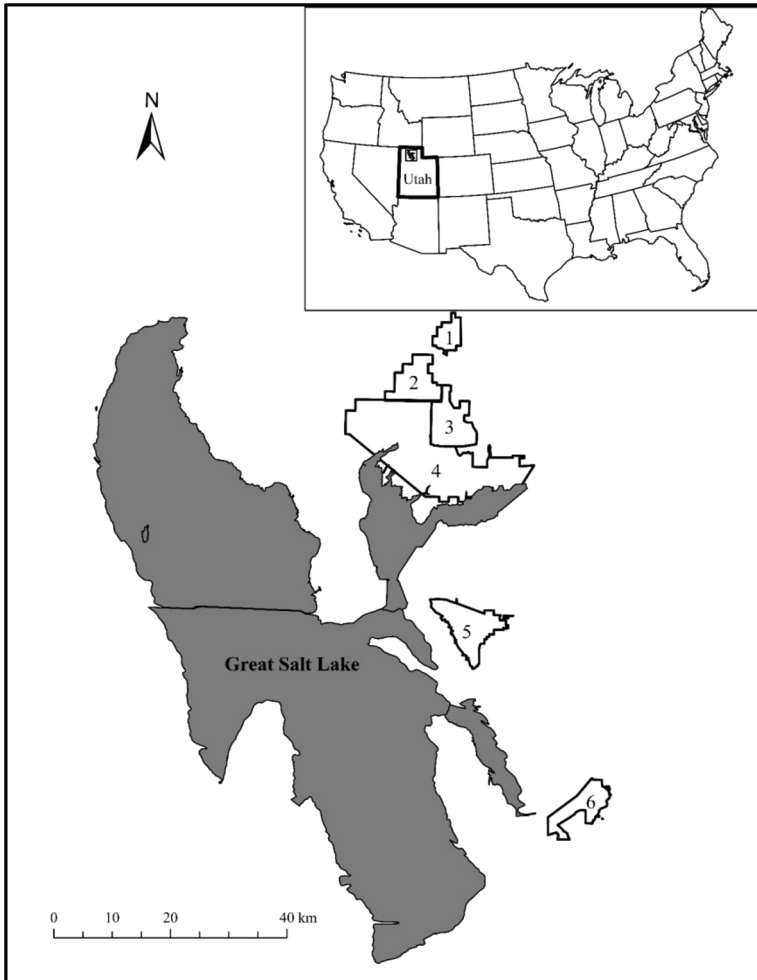
Figure 1. Study sites were located along the eastern shore of Great Salt Lake in northern Utah, USA in Waterfowl Management Areas (WMA). Shown on the map are: (1) Salt Creek WMA, (2) Public Shooting Grounds WMA, (3) Bear River Duck Club, (4) U.S. Bear River Migratory Bird Refuge (5) Ogden Bay WMA and (6) Farmington Bay WMA.

2.2. Methods

We searched for nests at these management areas during May-August, each year. Searches were conducted between 09:00–15:00 h Mountain Daylight Time, as recommended by Gloutney et al. (1993). We located nests on the dams using a modified chain-dragging method (Klett et al., 1986). A boom

was constructed out of lumber (3.8 × 8.9 cm, commonly referred to as 2 × 4 s), which extended 4 to 6 m out of the side of a pickup bed. We searched each side of the dam separately by searching 1 side as we headed along the dam away from the starting point and searched the opposite side as we came back towards the starting point. The length of boom was adjusted to accommodate the width of the dam being searched. Chains were attached to the boom and spaced approximately 25 cm apart. These chains were 8–12 m in length and dragged straight behind the boom as the truck drove at 10–15 km/h along the road running along the top of the dam. The chains flowed over and through the vegetation without creating a noticeable disturbance to the vegetation cover or nests. As the chains passed over or close to a nest, the incubating hen would flush, allowing an observer in the back of the pickup to locate the nest and identify the species of duck. The eggs were lower than the top of the nest bowl so that the chain did not touch them; only 1 egg was crushed by the chain during this study.

Once located, each nest received a unique number, and was marked by placing 2 survey flags with the unique identification number on the opposite side of the road to aid in relocating the nest for monitoring purposes. To limit odour deposition which might lead predators to the nest, only 1 investigator approached the nest and did so while wearing rubber boots. Time at the nest was kept as brief as possible and a new path was used to approach the nest during each revisit to avoid creation of a trial. We revisited nests every 2 weeks to determine their fate, and at the same time, we searched the dam for new nests. We used the same methods as Klett et al. (1986) to determine nest fate. We recorded fate as successful, depredated, or abandoned by observing the remains of the eggs after the nesting period was completed. A nest was considered successful if ⩾1 egg hatched. Hatched eggs have intact membranes separated from the eggshell walls. We recorded eggs that were crushed or opened without a detached membrane as depredated. A nest was considered abandoned if the eggs were cold, appeared undisturbed by a predator, and were unattended by a hen for >2 consecutive visits to the nest (Klett et al., 1986). We counted the number of eggs during each visit to the nest to determine if the number of eggs had changed, and the date of each count was recorded.

At each nest, we installed an infrared motion triggered camera (Cuddeback 20 Megapixal IR, Cuddeback, De Pere, WI, USA) capable of taking pictures day and night when triggered by movement (Croston et al., 2018;

Kruger et al., 2018; Blythe & Boyce, 2020). Cameras were placed approximately 40 cm away from the nest. We adjusted the camera height above the ground so that the camera was below the surface of the surrounding vegetation to decrease visual clues of nest locations. We set the downtime between each picture to 45 s to limit the number of repeat pictures taken of each event and to preserve memory card space. Camera images were used to confirm if a nest was successful or depredated. These images also were used to identify the species of predator that depredated the nest, as well as the timing, duration, and frequency of depredation events, and the response of the hen to its nest being depredated. We compared the time when cameras observed predators at nests with the egg counts before and after a depredation event to determine how many eggs were removed by a predator during a depredation event. We recorded the first predator species to depredate a nest. We then tallied the number of return visits made by that species to that nest and the elapsed time between visits. Camera detections of the same species that were separated by 1 h were counted as separate depredation events.

For each depredation event, we recorded air temperature, wind speed, humidity, whether the moon was above the horizon at the time of the event, the phase of the moon on the night of the event, and the proportion of the moon that was illuminated by the sun, and the cloud cover at the time of the event. We searched for these data on a website that stores historical weather records (weatherspark.com). We obtained the information from the Ogden-Hinckley Airport reference site, which was within 55 km of all study sites. We created a paired control for each initial depredation event by selecting a random day ±14 days (a full lunar cycle) from the depredation event. We then selected a random hour during the selected control night (21:00–06:00) and collected the same weather and light data for each control period. We separated the initial depredation events and their paired controls into those that occurred during the day, night and nautical twilight. The latter extended from before sunrise and after sunset until the centre of the sun was 12° below the horizon (National Weather Service). At that point in time, there was still enough light to see the horizon faintly, and the brightest stars were visible.

We used the average time of sunrise (06:00) and sunset (21:00) during May–July at our study area to establish depredation events between 06:00–21:00 h (Mountain Daylight Time) as events during the day, 22:15–04:45 h as events during the night, events during 04:45–06:00 h and 21:00–22:15 h as events during twilight. During our study in northern Utah,

the day was 15 h long, night 6.5 h, and twilight was 2.5 h (75 min before sunrise and 75 min after sunset). We compared the number of depredation events during the day, nautical twilight, and night to what would be expected if depredation events occurred randomly during a 24-hour period: 63% of them should occur during the day, 27% during night and 10% during twilight.

We created a variable called actual moonlight illumination to quantify what percentage of the moon was illuminated and what proportion of that light made it past the cloud cover. For each depredation event and control event, we determined if the moon was above the horizon at the time of the depredation event. If not, actual moonlight illumination was recorded as 0. If the moon was above the horizon during the depredation event, we multiplied the proportion of the moon illuminated on that night by the amount of open sky at the time of the depredation event.

2.3. Statistical analysis

Analysis was conducted using R (R Core Team, 2020). Data were pooled for all duck species and across all years to conduct statistical tests. This increased sample size for each test and was appropriate because nests of the different species were interspersed on the dikes and each species has a similar nesting ecology (Croston et al., 2018).

The timestamp when a predator was first observed by the nest camera was used as the time of each depredation event. We calculated the length of depredation events by subtracting the time of the last predator detection on the nest camera from the first sighting of the predator. For events only detected with 1 picture, we assigned a length of 1 min. We used 1-way ANOVA tests (Little & Hills, 1978) to compare event lengths across predator species. We used 1-tailed statistical tests because we were testing specific predictions about the behaviour of predators and ducks; results were considered statistically significant if $p < 0.05$.

We wanted to determine how frequently a predator returned to a nest that it had depredated in the past. We cannot know for certain that the same individual predator was returning to the nest, but we assumed that often times it would be the same individual returning to a nest and recorded this occurrence as such. For each nest depredated by a raccoon, we counted the number of times a raccoon returned to the depredated nest. For each nest depredated by a skunk, we counted the number of times that a skunk

returned to the depredated nest. The number of return visits to depredated nests was not normally distributed, so we compared the number of returns to depredated nests made by raccoons and skunks using a Mann–Whitney U-test (Siegel, 1956).

We recorded how often a hen returned to a depredated nest and the elapsed time from when the first predator left the nest until when the hen first reappeared. We used 1-way ANOVA tests to assess whether hens remained away from their nests longer depending on which predator depredated the nest. We tested whether the number of days a hen had incubated its nest prior to a depredation event had any influence on if it returned to its nest using a Mann–Whitney U-test. We also used a Mann–Whitney U-test to compare the number of eggs remaining in the nests of returning hens to the number of eggs remaining in nests of non-returning hens.

We predicted that predators would find depredated nests faster than an incubated nest because the former would have a smell of broken eggs. To test this, we used a 1-way ANOVA to compare the elapsed time between the first and second depredation event at the same nest to the elapsed time between when we found the nest and when it was first depredated. We used a 1-way ANOVA to compare raccoons to skunks in the number of eggs removed during a depredation event or the number of intact eggs remaining after it. For analyses involving egg counts, we only included nests that had a single depredation event between two consecutive nest checks because, for the nests with multiple depredation events, we were unable to conclude how many eggs remained or were destroyed after each of the depredation events. Using this procedure, 36 nests had a single depredation event in between two nest checks, 29 of which were depredated by raccoons or skunks, and were included in this analysis.

We used 1-way ANOVA tests to compare the depredation events with their paired controls to determine if depredation events were more likely to occur when temperatures, wind speeds, or actual moon illumination were low, or when humidity was high. We used a Pearson's chi-square test to compare the proportion of depredation events that occurred during the day, night, and nautical twilight for skunks, raccoons, and avian predators. We calculated the expected value of events by multiplying the total number of depredation events by the proportion of the 24-hour period made up by the day, night, and twilight. We conducted this test again using only depredation events of skunks and raccoons during the night and twilight periods. We used a

Pearson's chi-square test to compare the proportion of events during the night that occurred during each of the four phases of the moon with the proportion we would expect if depredation events were random.

3. Results

We placed cameras on 164 nests (71 cinnamon teal, 38 mallard, 44 gadwall and 11 unknown nests). Of the 164 nests, 21% were successful (15 cinnamon teal, 7 mallards, 8 gadwalls and 4 unknown), 73% were depredated (50 cinnamon teal, 29 mallards, 35 gadwalls and 5 unknown) and 7% were abandoned (6 cinnamon teal, 2 mallards, 1 gadwall and 2 unknown). We observed predators at 99 of the 119 depredated nests; predators at 20 nests went undetected. Undetected predators resulted from the lack of the camera being triggered on occasion, but usually resulted when vegetation grew, was pushed, or was blown by wind in front of the camera lens when pictures were taken, and the pictures were unusable to identify the predator. Raccoons ($N = 44$ depredated nests) and skunks ($N = 43$) were the most common of the 99 nest predators recorded. Other predators that depredated nests included long-tailed weasels (*Mustela frenata*, 3 nest depredations), northern harriers (2), California gulls (2), Sandhill cranes (*Antigone canadensis*, 2), common ravens (*Corvus corax*, 1), coyotes (*Canis latrans*, 1) and red foxes (1). Predators visited many of the 99 nests with recorded predators multiple times, resulting in 321 depredation events being recorded (Table 1). No photos or videos showed a duck and a predator in the same frame, meaning that all incubated hens detected the approaching predator and flushed prior to its arrival at the nest. It also indicated that we have no evidence that a duck attempted to defend its nest from a predator.

Because the nest cameras could not see all the eggs in a nest, we could not use the recordings of depredation events to determine the number of eggs removed by a predator. Instead, we had to rely on our visits to the nest before and after a depredation event to determine the number of depredated eggs. Our visits could not occur more often than once a week without potentially influencing the fate of a nest. If multiple depredation visits occurred between 2 consecutive eggs counts, the nest did not qualify for our analyses of egg numbers. This reduced our sample size to 36 nests for comparing the number of eggs removed and remaining after each predator species depredated a nest. Both raccoons and skunks removed an average of 7 eggs from

Table 1.

Depredation of duck nests.

Number of times depredated	Number of nests
1	31
2	22
3	12
4	13
5	5
6	5
7	5
8	2
9	1
13	1
15	2

We placed 164 cameras on duck nests located in the wetlands of Great Salt Lake, Utah during the nesting seasons of 2015–2021. Of the 164 nests observed, 34 nests were successful, 11 nests were abandoned, 20 were depredated but the predator was not detected, and the remaining 99 were depredated with the camera recording $\geqslant 1$ depredation events. The 99 depredated nests with recorded visits were depredated a total of 321 times.

a nest per event; foxes removed 6 eggs from a nest; coyotes removed 6; cranes removed 5; weasels removed 1; and harriers removed 1. Gulls did not depredate any nests for which we could collect these data. The number of eggs depredated per event did not vary among raccoons, skunks, and all other predators combined ($F_{2,33} = 0.83$; $p = 0.44$). When only raccoons and skunks were included in the analysis, the number of eggs removed did not vary between the 2 species (Table 2).

The number of eggs remaining after a depredation event did not vary among raccoons, skunks, and all other predators combined ($F_{2,33} = 0.16$; $p < 0.86$). Raccoons left an average of 1 egg, skunks 1, coyotes 0, and foxes 3, cranes 0, harriers 9, and weasels 8. When only raccoons and skunks were included in the analysis, the number of eggs remaining did not vary between the 2 species (Table 2).

The average length of the first depredation event was 7 min for all predator species, 5 min for raccoon, and 9 min for skunk. There were 7 other predator

Table 2.

F-tests comparing the number and proportion of eggs depredated and the number and proportion of eggs left unharmed in the nest after depredation events by each predator species.

	Raccoon		Skunk		$F_{1,27}$	p
	$\bar{X}$	SD	$\bar{X}$	SD		
Number of eggs depredated	7.1	2.8	6.4	3.5	0.38	0.54
Number of eggs left unharmed	1.2	2.7	1.4	2.3	0.03	0.86
Proportion of eggs depredated	0.88	0.26	0.82	0.30	0.31	0.58
Proportion of eggs left unharmed	0.12	0.26	0.18	0.30	0.31	0.58

Average clutch size of nests depredated was 8 eggs for both raccoons and skunks. Sample size was low (29 nests) because we had to exclude any nest that was visited by more than 1 predator before we could confirm the number of eggs remaining in the nest.

species that depredated nests; however, they were far less common than raccoon and skunk. We found 1 fox that spent 25 min at a nest. The fox was likely removing eggs to cache over this length of time, but returning frequently enough that it was recorded as 1 depredation event. Harriers spent an average of 8 min depredating nests. Cranes spent an average of 4 min at the nests they depredated. Weasels spent an average of 3 min at a nest, depredating 1 egg and not returning. Gulls and ravens spent an average of 3 min to depredate a nest. We found 1 coyote that depredated a nest, and it spent 1 min at the nest. Length of depredation events did not vary among raccoons, skunks, and all other species combined ($F_{2,96} = 1.51$; $p = 0.23$). Similarly, length of depredation events did not vary between raccoons and skunks ($F_{1,85} = 2.64$; $p = 0.11$).

Of the 99 depredated nests, raccoons were the initial predator to depredate 44 nests, and skunks were the initial predator to depredate 43. A raccoon returned to 23 (52%) of the nests first depredated by a raccoon, and a skunk returned to 28 (65%) of nests first depredated by a skunk, a difference between species that was not significant ($\chi_1^2 = 1.44$, $p = 0.23$). Raccoons revisited 20 nests and averaged 2 returns to nests after the first depredation. Skunks revisited 28 nests, averaging 3 returns to nests after the first depredation. The variation in the number of revisits between raccoons and skunks was not significant ($Z = 1.45$, $N = 48$, $p = 0.15$). Gulls returned to depredated nests the most, with an average of 6 times. Skunks found a nest after a raccoon had already depredated the nest 5 times out of the 44 nests first depredated by raccoons. Likewise, raccoons found a nest after a skunk had

already depredated it 5 times out of the 43 nests first depredated by skunks, showing no difference between in the number of times each species found a nest after the other species had already depredated a nest ($\chi_1^2 = 0.001$, $p = 0.97$). The length of time for a nest to be found after it had already been depredated ($N = 68$, 2.8 ± 4.1 days) was significantly shorter than the time it took for nests to be located by the initial predator ($N = 99$, 5.7 ± 6.0 days; $F_{1,165} = 11.61$; $p < 0.001$).

Of the 99 hens flushed off their nests by predators, 21% returned (14% of cinnamon teal, 27% of mallards, and 33% of gadwalls); these differences among species were not significant ($\chi_2^2 = 0.12$, $p = 0.94$). Hens were away from their nest a mean of 33 ± 72 h after a raccoon visited the nest and 23 ± 43 h after a skunk visit. This difference was not significant ($F_{1,19} = 0.13$; $p = 0.72$). Cinnamon teal hens remained off their nest 59 ± 89 h after a depredation event, mallards remained away 15 ± 14 h, and gadwall remained off their nests 3 ± 3 h after a depredation event. The length of the delay to return was not significant among duck species due to high variation among individuals within each species ($F_{2,18} = 1.93$; $p = 0.17$). Of the 21 hens that returned to their depredated nest, 17 of them incubated the depredated nest, but waited an average of 28 h after their nest was depredated before resuming incubation. The proportion of hens that incubated the depredated nests was not impacted by which predator species depredated the nest ($\chi_1^2 = 0.07$, $p = 0.80$) or by the species of duck ($\chi_2^2 = 0.40$, $p = 0.82$).

We predicted that hens would be more likely to incubate their depredated nest if it contained many eggs versus just a few or if the eggs were close to hatching versus eggs that just started to be incubated. We found that the number of eggs remaining in depredated nests was similar ($Z = 0.46$, $N = 36$, $p = 0.32$) between nests where the hen did not resume incubation ($\bar{X} \pm SD$, 1 ± 3 eggs), and nests where the hen did resume incubation (1 ± 2 eggs). Hens that resumed incubating their depredated nest had incubated their nest an average of 5 days prior to the depredation event while hens that failed to incubate their depredated nest had incubated their nest an average of 6 days prior to the depredation event; a difference that was not significant ($Z = 0.07$, $N = 99$, $p = 0.38$).

Only 1 of these depredated nests went on to be successful, a gadwall nest that was depredated by a skunk. Predators often returned to the nests of hens that resumed incubation, scaring them off their nest again. Of the 17 hens we observed incubating their depredated nest, 16 had their nest depredated

a second time and 6 incubated their nest after the second depredation. Of these 6 hens, three had their nest depredated a third time, and all three incubated their nest after the third depredation; the 1 nest successful despite being partially depredated was in this group. Of these 3 hens, two had their nests depredated a fourth time, and 1 incubated the nest after the fourth depredation.

We observed a total of 96 depredation events by raccoons and 121 by skunks because many nests were depredated multiple times. Raccoons made 57 visits at night, 20 visits during the day, and 19 visits during twilight with most visits occurring from 01:00–06:00 h (Figure 2). Skunks made 76 visits at night, 14 visits during the day, and 31 visits during twilight (Figure 3). Skunks exhibited bimodal visitation patterns with the first peak occurring in the hours before sunrise (04:00–05:00) and the second peak in the hours after sunset (22:00–24:00). Fourteen depredation events by birds occurred during the day, and five occurred near sunset (20:00–22:00). In contrast, there were no depredation events by birds during sunrise or the 3 hours after it (Figure 4). If depredation events were happening at random, 27% should occur during the night, 10% during twilight, and 63% during the day, given the number of hours in each period during a 24-hour cycle. The proportion
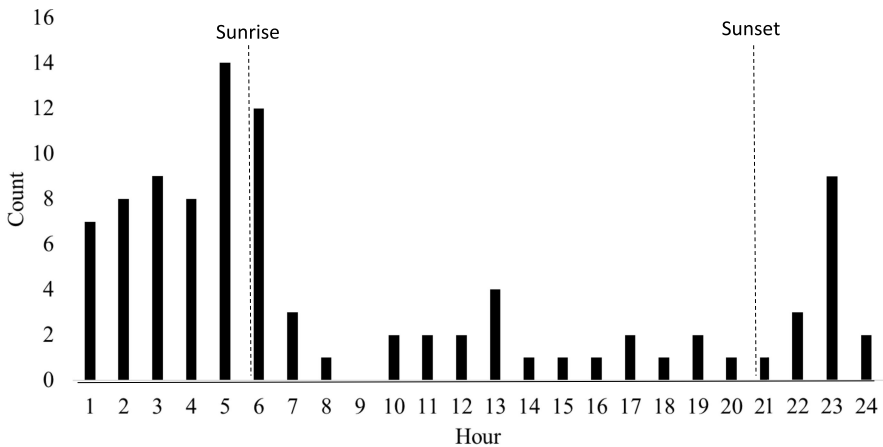

Figure 2. Number of nests depredated by raccoons during each hour of a 24-hour period, Great Salt Lake, Utah wetlands, 2015–2021. On average, sunrise occurred at 06:00 h, and sunset occurred at 21:00 h at the time of year when ducks were incubating nests. Nautical twilight lasted an average of 75 min before sunrise and after sunset in our study area during the study period.
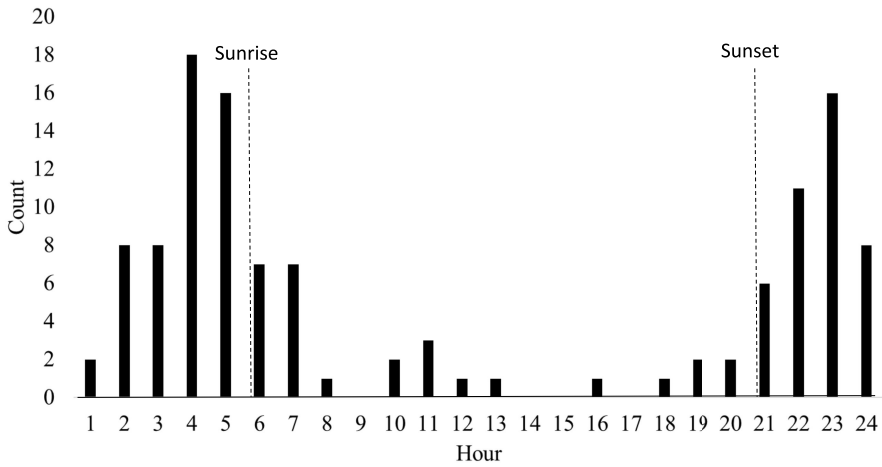
Figure 3. Number of nests depredated by skunks during each hour of a 24-hour period, Great Salt Lake, Utah wetlands, 2015–2021. On average, sunrise occurred at 06:00 h, and sunset occurred at 21:00 h at the time of year when ducks were incubating nests. Nautical twilight lasted an average of 75 min before sunrise and after sunset in our study area during the study period.

Figure 4. Number of nests depredated by avian predators during each hour of a 24-hour period, Great Salt Lake, Utah wetlands, 2015–2021. On average, sunrise occurred at 06:00 h, and sunset occurred at 21:00 h at the time of year when ducks were incubating nests. Nautical twilight lasted an average of 75 min before sunrise and after sunset in our study area during the study period.
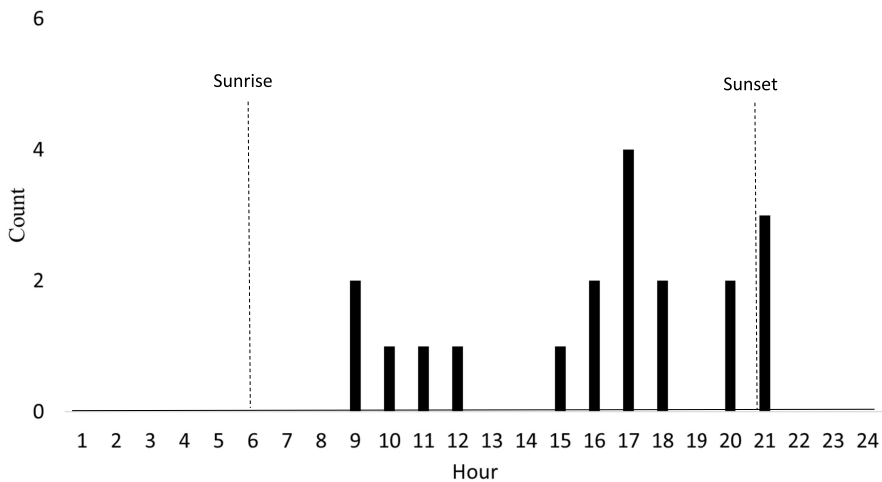
Table 3.

Results of 1-tailed paired t-tests comparing the temperature, humidity, wind speed and actual moon illumination during depredation events and paired controls occurring during the night hours ($N = 53$).

	Depredation events		Controls		T_{52}	p
	$\bar{X}$	SD	$\bar{X}$	SD		
Temperature (°C)	20	5	19	6	1.22	0.11
Wind speed (km/h)	12	6	14	6	1.89	0.03
Humidity (%)	38	15	38	17	0.04	0.48
Actual moon illumination (%)	33	40	28	40	1.04	0.16

Paired controls were created by selecting a random day within a full lunar cycle (28 days) centered on the depredation event and selecting a random hour during the night.

of occurrences of depredation events by raccoons ($\chi_2^2 = 35.07$, $p < 0.001$), skunks ($\chi_2^2 = 106.86$, $p < 0.001$), and avian predators ($\chi_2^2 = 7.12$, $p = 0.03$) during the 3 periods differed with what was expected if depredation events occurred at random.

Depredation events were more likely to occur when the wind was calm (Table 3). Temperature, humidity, and actual moon illumination had no effect. Moon Phase impacted when depredation events happened. Depredation events occurred more often during the 1st and 4th phases (the 2 phases around the new moon or when it was darkest) than during the 2nd and 3rd phases ($\chi_3^2 = 8.66$, $p = 0.03$).

4. Discussion

Prior to 1980 half of the world population of cinnamon teal (150 000) nested in GSL wetlands (Bellrose, 1980). Today, less than 10 000 cinnamon teal are estimated to use these wetlands (Olson, 2016). This shift indicates that these wetlands are no longer a safe or effective breeding ground for these ducks, pushing them to nest in other locations. Currently, most duck nests in the GSL marshes fail, and predators are responsible for most nest failures (Bell, 2022). In our study, raccoons and skunks depredated similar numbers of nests, and together were the greatest predators of nests in the GSL wetlands. This is a significant shift from the 1980s when Crabtree et al. (1989) reported that skunks were the main nest predator in the wetlands of GSL and that no nests were depredated by raccoons. The difference between our study and Crabtree's is that their study occurred before raccoons had expanded

their range to northern Utah and ours occurred after the arrival of raccoons. Croston et al. (2018) found raccoons depredated more nests than skunks in Suisun Marsh, California and showed raccoons can become a greater threat to nests than skunks. Larivière & Messier (2001) found skunks to be the principal predator of nests in Saskatchewan, Canada. Predators may have different effects across areas, but raccoons appear to be able to match or rise above the level of depredation pressure on nests by the native predators. The increase of depredation pressure in GSL wetlands appears to have suppressed nesting success.

Bell (2022) found in 2020 that raccoons were more abundant in BRMBR than skunks, and raccoons depredated a higher proportion of nests. However, in 2021, raccoons and skunks were of equal abundance and depredated equal proportions of nests. This suggests that both species are similar in their ability to find duck nests and in their preference for them over alternative foods available in GSL wetlands.

In our study, raccoons and skunks were active throughout twilight and during the night, with the highest activity occurring between 21:00–23:00 and 04:00–06:00 h before sunrise. Croston et al. (2018) found that most depredation by mammalian predators occurred between 20:00–23:00 and 01:00–04:00 h. However, Lariviere & Messier (2001) reported skunks were active between 02:00–06:00 h and did not find the bimodal activity pattern that we found for skunks. We found a small amount of depredation events by raccoon and skunk occurred during the day. In contrast, Urban (1970) reported raccoons rarely had movements during the day, meaning depredations would also be rare during the day. Similar to our study, Lariviere & Messier (2001) reported nearly one quarter of depredation events by skunk occurred during daylight hours.

We hypothesized that predators would spend little time at each nest and eat the entire clutch because their goal is to maximize food intake and to do it as quickly as possible to minimize the risk of another predator arriving. We found both raccoons and skunks only spent several minutes at a nest. Croston et al. (2018) also reported that raccoons and skunks remained at nests for short amounts of time. Predators such as raccoons and skunks are highly mobile and can cover lots of ground quickly. Given that these predators do not spend much time at each nest that they depredate, they have the potential ability to depredate many nests each night. In areas where nesting habitat

is limited or confined, such as GSL wetlands, these predators may have an increased ability to locate and depredate large numbers of nests.

We found that predators did not always consume an entire clutch of eggs during a depredation event, but usually left one or two undisturbed. It is unclear why raccoons or skunks would leave any eggs in a nest; perhaps the predator became satiated before consuming the entire clutch. Alternatively, it may be that the remaining eggs were rotten, and skunks and raccoons did not need to open the egg to determine this. Croston et al. (2018) reported that raccoons and coyotes typically removed most of a clutch during one event. Sargent et al. (1998) reported raccoons removing half of a clutch 1 night and returning to the nest to remove the remaining eggs over the next 10 days. Contrary to our findings, Croston et al. (2018) reported that skunks removed only 2–3 eggs per event; Lariviere & Messier (2001) found skunks destroyed <6 eggs per event. Both Croston et al. (2018) and Lariviere & Messier (2001) concluded that skunks likely became satiated sooner than other predator species. Red foxes are known to take eggs from a nest and cache them elsewhere (Sargent et al., 1998). Accordingly, we expected foxes to first eat their fill at a nest and cache the remaining eggs. Hence, we were surprised that foxes left an average of 3 eggs in the nest following a depredation event. In our study areas, predators den along or near (within 1 km) the same dams that hens nest on (Frey & Conover, 2006), giving these predators the opportunity to have repeated access to the same nests. Foxes leaving eggs in nests and not returning may be due to wariness or simply because there are many nests available to remove eggs from and it is not necessary to return to a particular nest to find eggs.

We hypothesized that each predator species would return to nests they had previously depredated to determine if anything edible remained or if the hen laid another egg in the nest. We also expected these subsequent visits to be shorter as the predator could quickly determine if food remained at the nest. We found many raccoons and skunks returned to depredated nests night after night. On subsequent trips, the predator would briefly inspect the nest and then leave, spending no more than a minute at the nest. Because we cannot individually identify these predators, it is not possible to determine if revisits were by the same individual that initially depredated the nest or a different individual of the same species.

All ducks were able to detect an approaching predator and flushed from the nest before the predator arrived. We found no evidence that a predator

killed a hen. No duck was observed trying to defend its nest from a predator. Raccoons can kill any duck that they can capture but skunks cannot. Hence, we expected that some incubating hens would try to defend their nests from skunks, but this was not the case. Many ducks that lose a clutch to a predator will select a new nest site and renest, especially if the eggs were lost early in the incubation period (Bellrose, 1980). We were unable to determine how frequently this occurred because ducks were not banded.

A hen that had already spent time incubating had invested large amounts of time and energy into its clutch. Hence, we hypothesized that hens would continue incubating any eggs remaining after a depredation event but only 21% returned to their nests after the first depredation event occurred, and only 17% resumed incubation. The hens must be making the decision of whether to resume incubation or to leave the nest based on the condition of the nest. Hens remained away from nests longer after a raccoon depredated the nest than when skunks depredated the nest. Hens may be warier of returning to a nest depredated by a raccoon than a skunk because the latter do not pose as great a risk to the hen's life as a raccoon (Bellrose et al., 1964; Sargent et al., 1998). Croston et al. (2018) noted a similar pattern, showing a growing consensus that these invading predators can have a drastic effect on the behaviour of hens and not just on nesting success rate.

When a hen is chased off its nest by a predator, the hen does not know the condition of the nest or the number of eggs remaining. The length of time the nest is left unattended by the hen after the nest is critical as any surviving eggs that are still viable may be exposed to high or low temperatures that could be fatal to the embryo. We hypothesized that hens would return quickly after a depredation event to resume incubation and care of their nest, but his was incorrect. Hens were away from their nest 33 h after a raccoon visited the nest and 23 h after a skunk visit. However, hens may have returned sooner to an area near the nest but only viewed the nest from a distance and were not photographed. Croston et al. (2018) reported hens returning to their nests much sooner than we found; this may reflect the danger posed to hens in GSL wetlands by the large predator community present in the narrow, linear habitat. Hens may be more wary when of returning to their nests when they perceive the constant presence of predators, especially in the narrow, linear habitat found in GSL wetlands where the predators can use the roads along dams to move efficiently throughout their home ranges and nests can never be more than 20 m from the road.

Predators hunting at night often rely on their sense of smell to locate prey. We hypothesized that depredation events at night would occur more frequently when winds were mild, temperature was low, and humidity high because these conditions made it easier to locate a nest using olfaction (Conover, 2007). We found wind speed was a factor affecting when depredation events occurred, with winds being slower during depredation events than during control events. Mild winds spread an odour plume and allow predators to easily follow the trail, however stronger winds that cause turbulence will make it more difficult for predators to follow the trail. Ruzicka & Conover (2011) found predators were less likely to forage when wind speeds were high enough to cause turbulence. Similarly, Webb et al. (2012) found wind velocity to be a significant factor affecting whether predators found nests.

We found no relationship between depredation events and temperature and humidity. Fogarty et al. (2017) found humidity to be positively associated with nest survival in their study of northern bobwhite (*Colinus virginianus*) in Oklahoma. We predicted that skunks and raccoons would be more likely to hunt, and therefore, depredate nests when nights were dark because prey that rely upon vision to detect predators will be disadvantaged by the reduced amount of ambient light. We found no correlation with the amount of moon illumination and depredation events during the night. Similarly, Symmank et al. (2014) reported that the percentage of moon illumination had no effect on raccoon activity during the night. Raccoons are omnivores and seek food opportunistically from both aquatic and terrestrial sources (Gaines et al., 2002) allowing them to forage any given night and not only on dark nights when it may be beneficial to search for duck nests. In our study, depredation events at night were more common during the 1st and 4th phases of the moon, which occur immediately before and after the new moon. Olfactory predators may be more likely to forage at night around the new moon because prey that rely upon their vision to detect an approaching predator would be disadvantaged. In contrast, Symmank et al. (2014) showed moon phase had no effect on nocturnal activity of raccoons in eastern Texas forests. Similarly, Springer (1982) found no change in movements of coyotes based on moon phase in south-central Washington.

Ackerman et al. (2003) suggests that managers should include an estimate of egg success in depredated nests into models to assess more accurately

waterfowl production. In our study, some hens returned to their nest to incubate the remaining eggs after a depredation event, but only 1 of these nests was successful indicating that the incubation of depredated nests contributed little to duck recruitment. This result shows not all areas should assume a particular success rate for partially depredated nests, and that a partial success rate likely varies among areas and years. It would only be beneficial for a manager to include an estimate of partial nest success in models for their management area if they have first found, and substantially validated, an estimate of partial success in their management area.

We cannot draw direct cause-and-effect conclusions from our observational study. However, we can find the relationship between measured variables and behaviours of predators and hens at depredated nests. Our study was limited because the nest cameras could not see all the eggs in a nest, and therefore, could not be used to determine the number of eggs removed by a predator during a depredation event. Instead, we had to rely on our visits to the nest before and after a depredation event to determine the number of eggs that had been depredated. Our visits could not occur more often than once a week without potentially influencing the fate of a nest. If multiple depredation visits occurred between 2 consecutive eggs counts, the nest did not qualify for our analyses of egg numbers. This reduced our sample size for this part of the study to 36 nests.

4.1. Conclusion

We found that in recent years since expanding their range into the GSL wetlands, the threat by raccoons to nesting ducks has risen to the same level as skunks. Together, the native and novel predators overwhelm nesting ducks and depredate most nests in GSL wetlands. Managers concerned with increasing nest success in these wetlands should focus efforts on controlling these two predator species. Few nests were partially successful after being depredated. Predators were most active during the 1st and 4th phases of the moon, indicating this as the time when managers may benefit from their removal efforts the most.

Acknowledgements

University, Utah Agricultural Experiment Station, and the Ecology Center of Utah State University. We thank C. Cranney, J. Jones, and R. Hansen for allowing us access to the state-run WMAs. We thank E. Holmes, M. Dunphy, and J. Wright for allowing us access to the U.S. Bear River Migratory Bird Refuge and answering our numerous questions. We thank C. Stettler for allowing me access to the Bear River Duck Club property. We are grateful to our summer technicians T. Larkin, L.E. Jeppsen and L.K. Anderson for their hard work helping us find, monitor, and record nesting data including many tedious hours of sifting through pictures and videos from the nest cameras.

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