Vertebrate Scavenger Species Composition on Nantucket Island, Massachusetts and Implications for *Nicrophorus americanus* Olivier (American Burying Beetle) Reintroduction

Andrew Mckenna-Foster[1,*], Danielle O'Dell[2], Elisabeth Sorrows[1], Jacqueline Laurenzano[1], and Lou Perrotti[3]

Abstract - We surveyed scavenger species on Nantucket Island, MA, using motion-activated wildlife cameras baited with carcasses of either a *Mus musculus domesticus* (House Mouse) or *Colinus virginianus* (Bobwhite Quail) in the summer of 2016. We aimed to identify vertebrate scavenger species, measure how long carcasses remained available, and examine differences in carrion consumption between grassland and shrubland vegetation types. This information is important for management decisions concerning a reintroduced population of a federally endangered obligate scavenger, *Nicrophorus americanus* (American Burying Beetle), on Nantucket Island. Carcasses were removed or consumed within 2.7 ± 1.8 d, and vertebrates removed the carcass in 74% of trials. Carcasses persisted for similar lengths of time between the 2 vegetation types, but avian scavengers were significantly more common on Bobwhite Quail carcasses in grassland, and mammalian scavengers were significantly more common on House Mouse carcasses in shrubland habitats. Avian species appear to be significant competitors for carrion appropriate for American Burying Beetle reproduction.

Introduction

Nantucket Island, MA, is the location of 1 of only 2 successful reintroductions of the federally endangered beetle, *Nicrophorus americanus* (Olivier) (American Burying Beetle, hereafter ABB) (Mckenna-Foster et al. 2016). The ABB is North America's largest carrion beetle (family *Silphidae*) with individuals up to 3.5 cm in body length. As a scavenger species, the ABB requires for reproduction a vertebrate carcass of 80–200 g, and the species is a direct competitor with vertebrate and invertebrate scavengers (Kozol et al. 1988, Raithel 2000). A beetle must find a carcass before it has been degraded or removed by other scavengers, attract a mate, and then bury the carcass in the soil. In one of the few examples of bi-parental care among non-social terrestrial insects, the beetle pair then rears up to 30 larvae on the carcass (Raithel 2000). The US Fish and Wildlife Service reintroduced captive-reared ABBs to Nantucket Island each summer between 1994 and 2006, and assisted the growing population in the following years through a regime of trapping in situ individuals, pairing them, and, in a process called provisioning, burying these pairs with vertebrate carcasses near the trap sites (Mckenna-Foster

[1]Maria Mitchell Association, 4 Vestal Street, Nantucket, MA 02554. [2]Nantucket Conservation Foundation, PO Box 13, Nantucket, MA 02554. [3]Roger Williams Park Zoo, 1000 Elmwood Avenue, Providence, RI 02907. [*]Corresponding author - andrew.mckennafoster@gmail.com.

Manuscript Editor: Christopher M. Heckscher

et al. 2016). This project is considered to have been successful because the trapping and provisioning methods appeared to increase the ABB population each year (Mckenna-Foster et al. 2016). However, carrion provisioning was reduced by 75% in 2011 and the population began a steady decline through 2016, which raised the question of whether ABBs are able to compete with Nantucket scavengers for naturally available carrion (Mckenna-Foster et al. 2016). The ultimate goal is to establish a self-sustaining ABB population on Nantucket; thus, it is critical that managers understand the scavenger community on this isolated island and its impacts on carrion availability.

Scavengers and the vertebrate carrion they consume significantly affect nutrient cycling (Wilson and Wolkovich 2011), community structure (e.g., Vucetich et al. 2004), and local biodiversity (Barton et al. 2013). Scavenging systems remain understudied, especially in the case of small vertebrate carrion (*Procyon lotor* (L.) [Raccoon]-sized or smaller), due to the difficulty of censusing natural carrion resources, complex interactions between facultative and obligate scavengers, and variability in scavenger composition across vegetation communities and seasons (Beasley et al. 2016, DeVault et al. 2003, Turner et al. 2017). In the last 2 centuries, loss of habitat, reductions of apex predators, increases in mesopredator populations, species extinction, and species invasion have changed the composition of vertebrate scavenger species and carrion resources in North America (Beasley et al. 2016, Prugh et al. 2009). Habitat fragmentation has helped 60 percent of North American mesopredator species expand their ranges (Prugh et al. 2009), and these species decrease local populations of small prey (Crooks and Soulé 1999) and monopolize carrion resources (DeVault et al. 2011). These changes are assumed to be partly responsible for a 90% reduction in the range and population of the ABB starting in the early 20th century (Sikes and Raithel 2002). Today, the ABB faces intense competition from vertebrate scavengers. In North America, vertebrate scavenging efficiency (percent of available carcasses utilized by vertebrate scavengers) averages 75% and can be up to 90% (DeVault et al. 2003). In agricultural landscapes, small carrion is usually consumed by vertebrates within 3 d (DeVault et al. 2004), and much of the scavenging is dominated by mesopredator species like Raccoons and *Didelphis virginiana* (Kerr) (Virginia Opossum) (DeVault et al. 2011). Persistence time may be longer in natural landscapes. Turner et al. (2017) recorded *Rattus* spp. (rat) carcasses persisting an average of 3.3 d and DeVault et al. (2017) recorded *Colinus* spp. (quail)-sized bird carcasses persisting for 7–9 d. Finally, Conley et al. (2015) found some evidence that mesopredators are more dominant scavengers in forested sites and at night, while avian species are more common in grasslands and during the day. Those authors suggested that there is both temporal and habitat partitioning between the 2 groups.

Nantucket was chosen as a reintroduction site for the ABB as part of a federal recovery plan partly because the island lacks common North American mammalian mesopredators, including Raccoons, Virginia opossum, *Vulpes vulpes* (L.) (Red Fox), *Urocyon cinereorgenteus* (Schreber) (Gray Fox), and *Mephitis mephitis* (Schreber) (Striped Skunk), all of which are assumed competitors of the ABB on the mainland (DeVault et al. 2011, Sikes and Raithel 2002). It is believed that Native American and early European inhabitants of the island extirpated these mesopredators (Zube and Carlozzi 1967), though since that time, both *Felis silvestris catus* L. (Domestic Cat) and *Rattus norvegicus* (Berkenhout) (Norway Rat) have established populations on the island. As a reproductively obligate scavenger species, the ABB competes for carrion resources with invertebrate, mammalian, and avian scavengers, and it is difficult to predict what conditions help the ABB succeed.

A growing body of literature on scavenging ecology from natural and agricultural settings suggest that the fate of a carcass and the scavenger species utilizing that carcass are influenced by a combination of biotic and abiotic factors. Higher temperatures inhibit vertebrate scavenger species and promote invertebrate scavenging (Beasley et al. 2016, DeVault et al. 2011), and micro-site variation in temperature and humidity may significantly affect the rate of carcass decomposition (e.g., Parmenter and MacMahon 2009). The type of carcass influences how long it persists and which scavengers will consume it; predator carcasses are consumed at a lower rate than other vertebrates (DeVault et al. 2017), and scavengers may avoid conspecific carcasses (Olson et al. 2016). Carcass size affects both scavenger community composition and carcass longevity. Smaller carcasses attract smaller mesopredators and persist for a shorter amount of time (Turner et al. 2017). Both Turner et al. (2017) and Abernethy et al. (2016) provide evidence that habitat type interacts with carcass type and scavenger species to influence carcass detection and longevity. Turner et al. (2017) found that scavengers detected *Sus* sp. (pig) carcasses significantly faster than smaller carcasses in a clear-cut habitat compared to forested habitat. However, smaller carcasses (e.g., rat and rabbit) were detected at the same rates across habitats.

Combining what is known about scavenging ecology with scavenger data from Nantucket could inform new management strategies to establish a self-sustaining ABB population on the island. Understanding the fate of a carcass on the island is a first step in this process. Managers need site-specific information on scavenger composition and scavenger efficiency from vegetation types utilized by the ABB. The goals of this study were to (1) understand which scavengers were competing with ABB in 2 common vegetation types, and (2) determine carcass persistence and vertebrate scavenging efficiency for a carcass suitable for use by the ABB in 2 common vegetation types. Nantucket lacks most mesopredators; thus, we hypothesized that avian species would dominate the scavenger community. Based on other studies, we predicted *Corvus brachyrhynchos* (American Crow), *Cathartes aura* (Turkey Vulture), and *Cyanocitta cristata* (L.) (Blue Jay) would be common visitors to carrion (DeVault et al. 2004, 2017; Olson et al. 2016). We also hypothesized that carrion in shrubby vegetation would be more difficult to detect and access and therefore persist longer than in grassland. There are no North American studies of systems that contain common avian scavengers but not the common mesopredators, so it was difficult to predict how a lack of mesopredators would affect carcass persistence or scavenging efficiency. Olson et al. (2016) saw avian species feeding on 60% of medium-sized carcasses (rabbit, Virginia

Opossum, or Raccoon), while DeVault et al. (2011) recorded avians scavenging only 8% of mouse or rat carcasses. Avians are regularly observed visiting carrion, and Nantucket has populations of many of the common avian scavengers; thus, we predicted carcass persistence and scavenging efficiency similar to mainland observations for small carrion.

Field-site Description

Nantucket Island lies 50 km south of Cape Cod, MA, and contains ~130 km^2 of sandplain grassland, coastal heathland, barrier beach, and mixed forest (Fig. 1). We selected camera sites within large tracts of conservation land that protect diverse sandplain grassland and coastal shrubland vegetation communities. *Quercus ilicifolia* Wangenheim (Scrub Oak) and *Pinus rigida* Miller (Pitch Pine) grow in small patches among a mosaic of low grasses and shrubs. The ABB range encompasses the eastern half of the island, where these 2 vegetation communities are common (Mckenna-Foster et al. 2016) (Fig. 1).

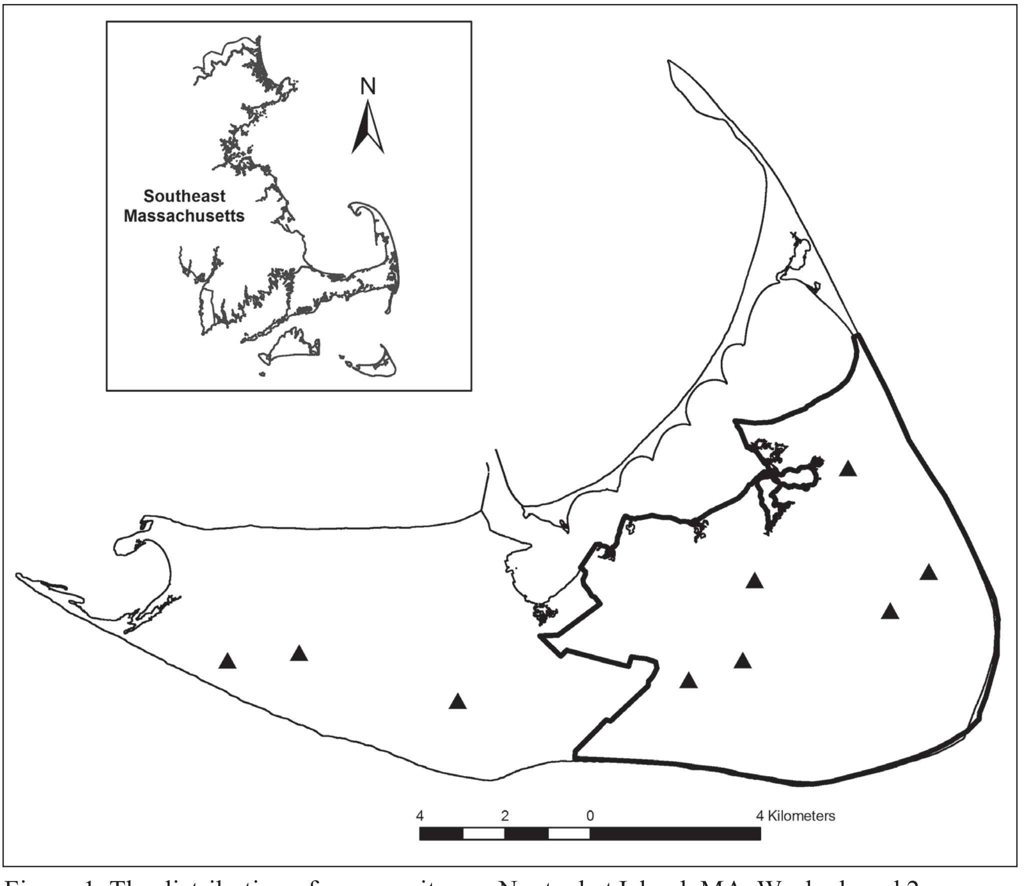

Figure 1. The distribution of camera sites on Nantucket Island, MA. We deployed 2 cameras at each sample site to identify scavenger species. Triangles represent sample sites and are not to scale. The dark boundary outlines the assumed range of *Nicrophorus americanus* (Olivier) (American Burying Beetle).

Methods

Between 22 June and 3 August 2016, we deployed 18 Browning BTC-5 wildlife cameras (Browning Trail Cameras, Birmingham, AL) in pairs at 9 sites across the island, and baited the camera stations weekly with either a deceased, dark-haired *Mus musculus domesticus* L. (House Mouse [hereafter Mouse], average mass = 32.4 g) or a *Colinus virginianus* (L.) (Bobwhite Quail [hereafter, Quail]; average mass = 132.6 g) (Fig. 1). We used Quail during the first 3 weeks to coincide with peak ABB reproductive activity and Mice the last 3 weeks to extend the study duration. While this change in carrion type and size likely affected which scavengers visited our sites, the focus of our study was a general species census for small-carrion scavengers rather than a determination of scavenger preferences for different carrion types. ABBs will feed on any available carrion, and Mouse-sized carcasses are a potential food resource (Raithel 2000). We placed all 6 of the eastern camera-trap sites near well-established ABB trap lines. We also placed camera-trap sites in potential ABB habitat on the west side of the island. At each site, we placed 1 camera in a grassland and 1 camera in closed-canopy shrubland, ~100 m apart. The cameras were generally within 10 m of a dirt road. We did not record temperature at each site, but as a proxy, report average temperatures recorded at the Nantucket Memorial Airport and retrieved from the National Oceanic and Atmospheric Association (NOAA 2018). Data from temperature logging iButtons (Maxim Integrated, San Jose, CA), placed at 5 of our camera-trap sites in June 2015, showed that the difference in ground temperature between the airport and our sample sites was <2 °C. The ground temperature at these sites was 5.1 ± 2.9 °C hotter in the daytime and 1.7 ± 1.4 °C cooler in the nighttime than the air temperature at the Nantucket airport.

We constructed wooden stakes to hold the camera over the carrion in the grassland sites. In the shrubland sites, we attached cameras to sturdy branches or used a wood stake when necessary. All cameras faced the ground from a height of 1–2 m. We secured the bait to a turf staple directly below the camera using dental floss tied to a rear leg to prevent the carcass from being carried out of the view of the camera. We replaced the bait and swapped out SD cards and camera batteries every 7 d. We also moved the cameras to a new location at least 100 m away from the previous week's location to reduce habituation to a static bait-station and more accurately mimic natural carrion availability. The cameras took 2 pictures per trigger event and waited 10 secs before resetting. Before placing the carcass underneath the camera, we trimmed the grass and small shrubs to reduce the chance of windblown vegetation triggering the camera.

We identified any animal seen in each picture frame, noted general behavior (moving through picture frame, standing, investigating carcass, actively consuming carcass), location of the animal in the picture frame in relation to the carcass, and the condition of the carcass. Small rodents visiting carcasses could be difficult to identify, especially in nighttime photographs, and when a positive identification could not be made, we recorded them under the general classification of "rodent". If the same species visited a carcass within 5 min, we assumed it was the same individual and recorded it as a single scavenging event. We considered a carcass to be consumed if it was either removed or if only bones, fur, or feathers remained. This decomposition stage was relatively easy to identify, and a carcass that reached this stage was generally left undisturbed by scavengers.

Results

The cameras took 69,835 photographs of which 2% contained a vertebrate or invertebrate species. Most photographs were triggered by moving vegetation or an unidentifiable trigger. Average daily temperature on the island each week in the study period was 20 ± 3 °C and varied from 18 to 23 °C (NOAA 2018). Due to equipment failures, we collected data from 87 of the 108 possible trials. A total of 43 trials used Quail carrion and 44 trials used Mice. We were able to identify which scavenger consumed the carcass in 65 trials (Table 1). In 19 trials, the camera did not photograph the scavenger that removed the carcass; in 2 trials, the carrion disintegrated as a result of general scavenging by vertebrate and invertebrate species; and in 1 trial the scavengers did not visit the Mouse carcass and it remained relatively intact the entire week. Vertebrates consumed or removed carrion in 74%

Table 1. Species that removed Mouse or Quail carcasses on Nantucket Island, MA. We classified carcasses that slowly degraded over time due to multiple scavengers and cases where the camera failed to capture the scavenger as "Unknown". The "Carrion beetles" classification represents cases where a variety of species in the families Scarabaeidae and Silphidae consumed the carcass. We used the "Unidentified insects" classification when a combination of flies, ants, and beetles consumed the carrion.

Scavenger	Quail	Mouse	Total
Mammals (35%)			
Unidentified rodents	4	6	10 (15%)
Peromyscus leucopus (Rafinesque) (White-footed Mouse)	3	5	8 (12%)
Rattus sp. (rat)	0	2	2 (3%)
Canis lupus familiaris L. (Dog)	1	0	1 (2%)
Blarina brevicauda (Say) Short-tailed Shrew	0	1	1 (2%)
Felis silvestris catus (L.) (Domestic Cat)	0	1	1 (2%)
Avians (39%)			
Corvus brachyrhynchos Brehm (American Crow)	7	4	11 (17%)
Buteo jamaicensis (Gmelin) (Red-tailed Hawk)	5	2	7 (11%)
Cathartes aura (L.) (Turkey Vulture)	6	0	6 (9%)
Circus hudsonius (L.) (Northern Harrier)	0	1	1 (2%)
Invertebrates (26%)			
Diptera spp. (flies)	3	2	5 (8%)
Unidentified insects	1	2	3 (5%)
Formicidae spp. (ants)	0	3	3 (5%)
Nicrophorus spp. (burying beetles)	1	2	3 (5%)
Silphidae spp. (carrion beetles)	2	0	2 (5%)
Nicrophorus marginatus Fabricius (Margined Burying Beetle)	0	1	1 (2%)
Subtotal	33	32	65
Unknown	10	9	19
Not scavenged	0	1	1
Multiple species	0	2	2
Total	43	44	87
Camera failed	12	9	21

of trials where we could identify the scavenger (48/65). It took an average of 2.7 ± 1.8 d for the carrion to be consumed in place or removed. There was no significant difference in the number of days it took scavengers to consume a carcass in shrubland or grassland sites (unpaired *t*-test: df = 78, $P = 0.44$). In 53% of trials, scavengers first made contact with a carcass within 12 h, and 92% of carcasses had been located within 36 h. The surrounding vegetation did not significantly influence the time to discovery (unpaired *t*-test: df = 86, $P = 0.10$).

We identified 9 vertebrate species removing carrion (Table 1). Five species or species groups accounted for 65% of scavenging events and all are species seen in mainland scavenger studies: American Crows, unidentified rodents, *Peromyscus leucopus* (White-footed Mouse), *Buteo jamaicensis* (Red-tailed Hawk), and Turkey Vultures. Many of the unidentified rodents were most likely White-footed Mice. We also observed species not often reported in other studies including *Circus hudsonius* (Northern Harrier) and Norway Rats. Domestic Cats visited 3 Quail carcasses, 2 in grassland and 1 in shrubland habitat, and removed 1 Mouse carcass from a grassland site.

We compared the number of carcasses removed by avians, mammals, or invertebrates overall and within each combination of carcass type and vegetation type (Fig. 2). Due to small sample sizes, we used the exact multinomial goodness-of-fit test in all comparisons (XNomial package; R Core Team 2013). There was no significant difference in the overall number of carcasses removed by avians (39%), mammals (35%), or invertebrates (26%) ($P = 0.45$). The proportion of carcasses removed by these 3 scavenger groups differed significantly for Quail carcasses in grassland and Mouse carcasses in shrubland ($P = 0.01$ and $P = 0.01$, respectively). Within these 2 categories, we performed a post hoc analysis using the exact binomial goodness-of-fit test with an adjusted alpha level of 0.02 (0.05/3). Avians scavenged significantly more Quail carcasses in grassland than expected ($P = 0.002$), while mammals scavenged significantly more Mouse carcasses in shrubland ($P = 0.002$). Overall, avian species removed a majority of Quail carcasses (55%) and mammals removed the largest percentage of Mouse carcasses (44%) though neither was significant (Quail: $P = 0.05$, mouse: $P = 0.25$).

No ABBs visited carcasses, although related species of *Nicrophorus* carrion beetles buried 3 Mouse carcasses and 1 Quail carcass (4.5% total). *Nicrophorus marginatus* (Margined Burying Beetle) buried 1 Mouse but we could only narrow the other burying events to either *N. marginatus* or *N. orbicollis* Say (Roundneck Sexton Beetle). Invertebrates consumed another 13 carcasses. In 10 of these cases, we could clearly identify flies, ants, or carrion beetles (representing a variety of species in the families Scarabaeidae and Silphidae) as the primary scavenger and ultimate consumer of a carcass.

Discussion

The scavenging community on Nantucket is comprised of avians, rodents, and invertebrates. In the absence of mammalian mesopredators, rodents and invertebrates consume a larger percentage of carcasses than reported elsewhere.

DeVault et al. (2017) recorded avians and mesopredators scavenging 28% and 67% of carcasses respectively, while Olson et al. (2016) recorded 41% and 57% respectively. Neither study observed rodents or invertebrates as significant scavengers. In our study, avians, rodents, and invertebrates each consumed about one third of the carcasses.

Our findings support the hypotheses that small carrion on Nantucket would both be scavenged primarily by vertebrates and at a similar rate as mainland carrion. Vertebrates scavenged 74% of carrion and carrion persisted for about 3 d, well within the ranges of values reported elsewhere (DeVault et al. 2003, 2004; Turner et al. 2017). Contrary to our expectations, carcasses in shrubland did not persist longer than carcasses in grassland. This result was due to the presence of an efficient

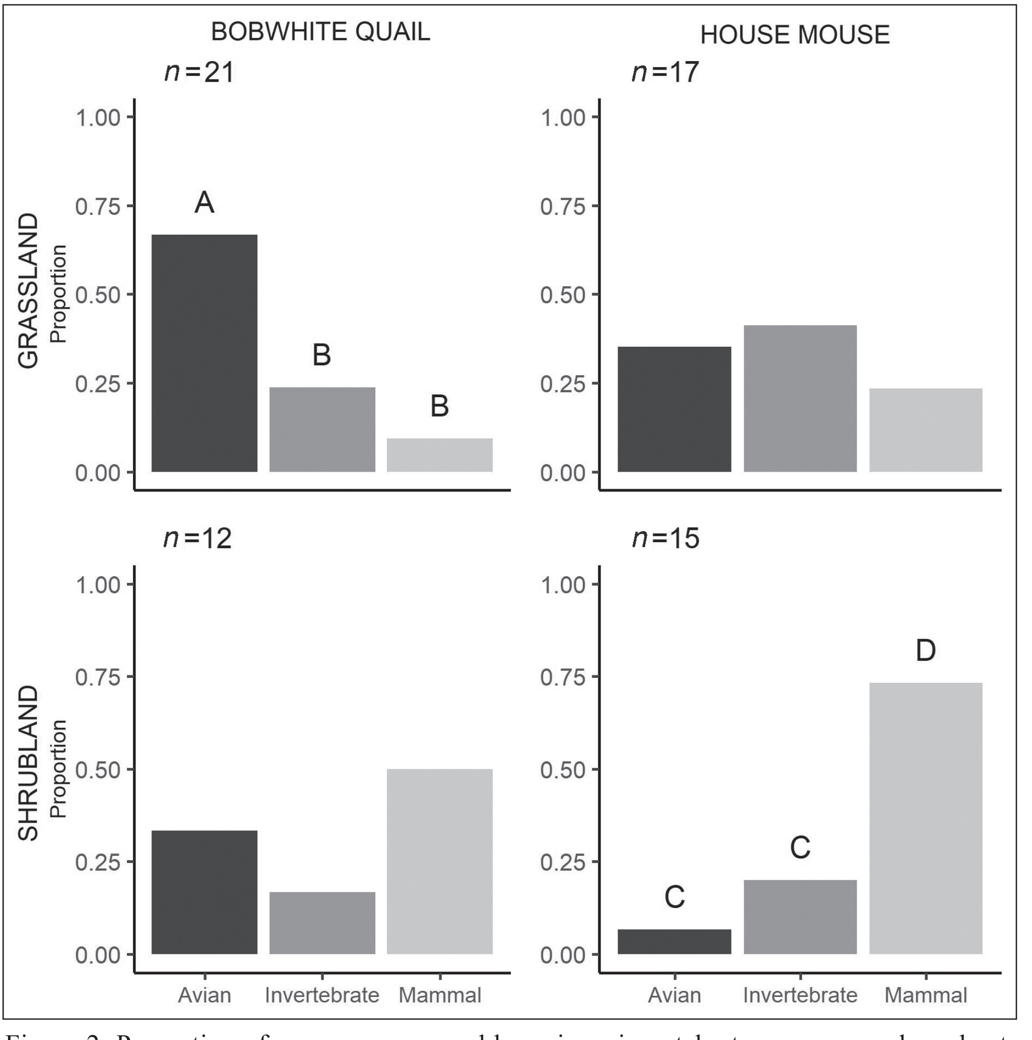

Figure 2. Proportion of carcasses removed by avians, invertebrates, or mammals and categorized by vegetation and carcass type. Letters identify significant differences. Avian scavengers removed significantly more Quail carcasses in grasslands, and mammals removed significantly more Mouse carcasses in shrublands.

community of rodent scavengers that consumed a significant number of carcasses in shrubland. Conversely, while we expected avian scavengers to dominate across vegetation types, they were only dominant on Quail carcasses in grassland, perhaps because these carcasses were easier to detect and access. Conley et al. (2015) found similar habitat partitioning among mammalian and avian species, though the mammalian species were all mesopredators.

Nantucket scavengers may be a more significant factor in establishing a self-sustaining ABB population than originally thought. During the peak ABB reproductive period in late June, avian species are the main competitor for carrion that is suitable for ABB reproduction. The high number of Quail carcasses scavenged by avians was largely due to Turkey Vultures, which we observed only feeding on Quail carcasses and only during the first 2 weeks of our sampling period. Red-tailed Hawk and American Crows were also common scavengers during that time, removing 4 Quail carcasses each. American Crows continued to regularly scavenge carcasses throughout the rest of the study. The ABB is reproductively active into mid-July on Nantucket and we assume American Crows and Red-tailed Hawks remain important consumers of Quail-sized carrion throughout this time. However, time and carcass type are confounding variables because we did not deploy Quail and Mice simultaneously. We cannot know from our data whether avians scavenged more Quail carcasses because of the time of year or because they prefer larger or non-mammal carrion.

In addition to vertebrate species, we found evidence that the ABB faces competition from other *Nicrophorus* beetles. *Nicrophorus* species compete both in the race to locate a carcass and in direct confrontation for a carcass. The ABB can compete well in direct confrontation (Kozol et al. 1988) but may be outcompeted by congener species in the search for carcasses (Matthews 1995). We attribute the lack of ABB sightings in our study to a small population size and the recruitment of beetles to monitoring pitfall traps set within the same study area. In June 2016, the monitoring traps captured 24 ABBs, the lowest number in 12 y of trapping (Mckenna-Foster et al. 2016). These traps were baited with odoriferous rotted chicken and were in some cases within 50 m of the camera sites, potentially attracting away the limited number of ABBs. Margined Burying Beetle and Roundneck Sexton Beetle are also attracted to the traps, but their populations are much larger than the ABB, increasing their chances for detection at camera sites (A. Mckenna-Foster, unpubl. data).

This survey provides important information to inform ABB management decisions. Despite a lack of mammalian mesopredators, the ABB on Nantucket faces similar levels of competition for its reproductive resource compared to what it might face on the mainland. Efforts to establish a self-sustaining ABB population will have to account for this effective scavenging community. Further work should investigate carcass-type preference for Nantucket scavengers and ABB success at locating carcasses in grassland and shrubland. ABBs can use a wide variety of carcass types (mammal or avian) for reproduction if the carcass is within the correct size range (Amaral et al. 1997, Kozol et al. 1988). It could be useful for managers to know if some types are scavenged at a lower rate compared to others. Avians and rodents appear to be more effective scavengers in grassland and shrubland, respectively; thus, understanding how the ABB uses those vegetation types on Nantucket could guide future recovery efforts.

Acknowledgments

This project was partly funded by grant #15-233 from the Norcross Wildlife Foundation. The Roger Williams Park Zoo, Providence, RI, generously provided Quail carcasses and field equipment. Alex Etkind, Skyler Kardell, Corrina Marshall, and David Ryan assisted with field work and photo processing. We thank Jennifer Karberg and 2 anonymous reviewers for providing valuable comments.

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