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Measuring success of a reintroduced population of the American burying beetle (*Nicrophorus americanus* Olivier) to Nantucket Island, MA

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Abstract The American burying beetle (*Nicrophorus americanus*) is a federally listed endangered beetle and since 1993 multiple organizations have collaborated to reintroduce this species to Nantucket Island, Massachusetts, USA. We present evidence that despite very successful reintroduction methods, the reintroduced population is not self-sustaining and requires human assistance for long term maintenance. Beetles were reintroduced from captive stock and each year we augmented the population by trapping wild beetles, pairing males and females, and supplying the pairs with carrion. Long term monitoring of this population has shown that, when provided with carrion, *N. americanus* on Nantucket have an over winter survival rate of 15 % and a reproductive success rate of 54 %. After seeing the number of beetles captured between 2007 and 2011 double, we modified protocols to determine if the established population would be self-sustaining and we have seen a drastic decline. We suggest that a lack of natural carrion is the main reason for this decline.

Keywords American burying beetle ·
Nantucket Island · *Nicrophorus americanus* ·
Reintroduction

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Introduction

The federally endangered American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae, hereafter ABB) is the largest of North America's carrion beetles and its historical range covered 35 states in the eastern temperate areas of North America (USFWS 1991). Today, populations remain in only eight states at the fringe of the historical range (USFWS 2016). Reasons for the decline of the species are not well understood but may include decreased carrion abundance, habitat change, increased competition from vertebrates and other carrion beetle species, and possibly disease (Sikes and Raithel 2002). The range of ABBs on the east coast is particularly limited and consists only of a population on Block Island, RI, and a reintroduced population on Nantucket Island, MA.

ABBs are one of 15 species in the genus *Nicrophorus* in North America (Peck and Kaulbars 1987), all of which reproduce by burying a dead vertebrate on which their larvae feed. ABBs are specialists using carcasses between 80 and 180 g, and show a high level of bi-parental care (Wilson 1971). In early summer, ABBs locate a vertebrate carcass, bury it and prepare it with anal and oral secretions to prevent decomposition. They raise a brood of 1–30 larvae in roughly 15 days, through three instars. These larvae then burrow into the surrounding soil to pupate. They emerge about 45 days later to feed in preparation for overwintering. They emerge the following spring to restart the process. Adults survive through one reproductive season. ABB research includes work on life cycle (Bedick et al. 1999; Schnell et al. 2008), local distributions (Carlton and Rothwein 1998; Bedick et al. 1999; Backlund et al. 2008), reproductive needs (Holloway and Schnell 1997), captive care (Kozol 1992), habitat preferences (Creighton et al. 1993, 2009), dispersal (Raithel et al. 2006; Creighton and Schnell 1998), and genetics

(Szalanski et al. 2000). However, the reasons for its decline and the factors that support a self-sustaining population and a successful reintroduction, are not well understood (Sikes and Raithel 2002).

In addition to promoting the long term survival of a rare species, reintroduced populations of rare species improve local biodiversity, restore the role of keystone species, and can be used to promote conservation awareness (IUCN 1998). Additionally, these restored populations can act as a genetic reserve when populations are susceptible to catastrophic disturbances (e.g. hurricanes), as is the ABB in its last remaining, single natural eastern population on Block Island. Although invertebrates are the focus of reintroductions around the world (Soorae 2010, 2011), they constitute a disproportionately low number of projects in comparison to other taxa (Seddon et al. 2005). A successfully reintroduced ABB population has great potential impact for the conservation of this species as well as other invertebrate species. Additionally, documenting successful and unsuccessful methods of invertebrate reintroductions may be useful for other invertebrate conservation projects.

Attempts to reintroduce the ABB have occurred on Penikese Island, MA (Amaral et al. 1997), Nantucket Island, MA (Mckenna-Foster et al. 2015), Ohio (Keeney and Horn 2005, 2007), and Missouri (Stevens et al. 2006; Merz 2014). Of these, the longest running program and one of the most successful to date, is on Nantucket. Nantucket Island is relatively isolated 40 km south of Cape Cod. The criteria that made it a viable reintroduction site include (1) a historical presence of ABBs (2) an assumed relative abundance of possible vertebrate carrion (primarily birds) (3) a lack of mammalian scavengers (4) a large area of protected land and (5) a favorable bio-political climate with multiple organizations willing to partner on the project (pers. comm. Christopher Raithel).

Prior to its reintroduction, the last known sighting of an ABB on Nantucket was in 1926 (Johnson 1930; Amaral 1993). In the summer of 1994, the U.S. Fish and Wildlife Service introduced 22 pairs of beetles and four individual females to Nantucket (Amaral 1998) with the ultimate goal of creating a self-sustaining population (USFWS 1991). Since then, the project has gone through three phases, each with different proximate goals. From 1994 to 2006, the goal was to establish and monitor the ABB population through releases of captive reared beetles and limited trapping of wild adults. Most beetles were reared from Block Island stock at the Roger Williams Park Zoo in Providence, RI, and some beetles were introduced directly from Block Island. From 2007 to 2010, introductions stopped and the goal was to boost the population by capturing, pairing and provisioning with carrion as many ABBs as possible. We hypothesized that without major human intervention, the population would decline. To test this, starting in 2011, the project moved to a phase of monitoring the population and provisioning a reduced number of beetles. In this paper, we critique our methodology, present an analysis of parameters affecting the Nantucket ABB population and assess its potential to be self-sustaining.

Methods

To determine population size, as well as capture adults for provisioning with carrion, we trapped ABBs during two periods each year, one in the early summer (approx. mid June) to overlap with the peak adult breeding season and another in the late summer (approx. early September) to sample juvenile emergence. We captured beetles using 1-l glass Mason jar pitfall traps baited with rotten chicken, following the protocol of Kozol (1991). We adjusted the numbers and geographic spread of traps as we identified successful sites and geographic areas where we needed additional data. Prior to 2007, trap sites usually had 20 traps arranged in a ~400 m line. Starting in 2007, to facilitate trapping over a broader area with the same amount of person hours, we reduced most trap sites to five traps, except for the main release site (20 traps) and two nearby sites, located centrally within the overall trapping area (ten traps each). The distance between trap lines was 2.6 ± 2.1 km. Consistency in trap number was not considered necessary for most of the project's history because the goal was to collect as many beetles as possible for pairing and provisioning. In 2013, and continuing to present, we began a more standardized trapping method with all sites consisting of five traps evenly spaced over 100 m and arranged uniformly across the eastern half of the island, with an average distance of 2 ± 0.7 km between sites (Fig. 1).

The U.S. Fish and Wildlife Service (2012) estimated that a line of eight small traps (such as 1-l Mason jars) has an effective radius of 0.8 km and while we use five traps per line, we believe it is similarly effective. Leasure et al. (2012) suggests that traps within a trap line are not independent and a few ineffective traps (whether from tampering or malfunction) do not significantly reduce the effectiveness of the trap line. Assuming the effectiveness of each site is a circle with a radius of 0.8 km, with some overlap between sites, the total sampling area on Nantucket was 26.7 km² in 2013 and 22.7 km² in 2014–2016 (Table 1). Trap area in years previous to 2013 was smaller, ranging from 5–19.5 km². Another way of measuring trap area is delineating the geographic area containing the trap sites. Assuming large bodies of water are a boundary to the ABBs and that the built up residential areas to the west are either boundaries or are collectively a population sink (due to lights at night attracting the beetles to unsuitable habitat), our trap sites sampled an area of ~64 km² (Fig. 1). Cold nightly temperatures do

Fig. 1 Trap area for American burying beetles on Nantucket Island, Massachusetts. The assumed geographic trapping area is bounded by water or heavy residential development and the gray buffers are the estimated effective range (0.8 km radius) for the five traps at each site
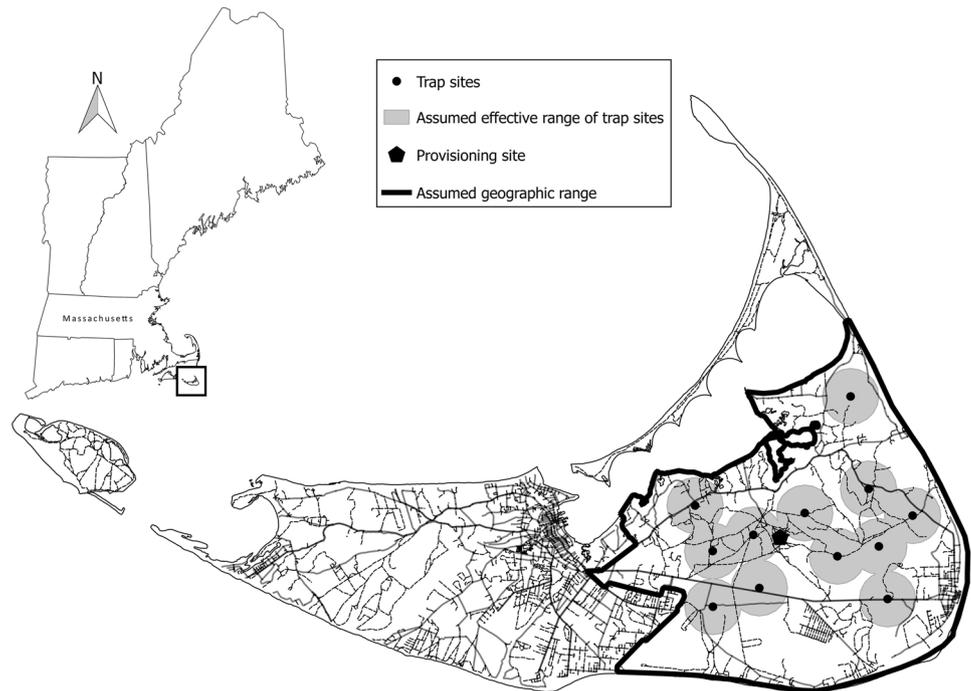
Table 1 Total early-summer trap nights and ABB captures with trap rates since 2004

Year	Total trap nights	Trap area km^2	Total number of wild ABBs	ABBs/trap night	ABB/trap area	ABB/geographic area (64 km^2)
2004*	360	6.3	33	0.092	5.2	0.52
2005*	480	6.3	38	0.079	6.0	0.60
2006*	640	8.3	50	0.078	6.0	0.78
2007	1022	19.5	97	0.095	5.0	1.5
2008	1348	19.5	112	0.083	5.7	1.8
2009	1791	19.5	150	0.083	7.7	2.4
2010	1663	19.5	191	0.115	9.8	3.0
2011	1011	19.5	212	0.210	11	3.3
2012	1237	19.5	115	0.093	5.9	2.0
2013	1386	26.7	52	0.038	1.9	0.82
2014	778	22.7	36	0.046	1.6	0.56
2015	880	22.7	32	0.036	1.4	0.50
2016	976	22.7	24	0.025	1.1	0.38

Wild ABBs refers to beetles that were not reintroduced from the zoo-reared population. Asterisks (*) indicate years when ABBs were reintroduced to the island from captive reared stock

affect ABB movement (and thus trap effectiveness) (Raithel et al. 2006) but since we continuously trapped over most of the reproductive season, we assumed available beetles would at some point be trapped and we did not subtract trap nights based on weather.

During the early-summer trapping, we sexed, weighed, measured pronotal width, and notched the elytra or pronotum of all captured beetles. We used a hand-held cauterizer to notch beetles in a pattern unique to each trapping site (Mckenna-Foster et al. 2015). Hall et al. (2015) suggest

that large elytral notching can affect reproductive success in ABBs. However, triangular notches used on Nantucket are only one mm wide on the caudal edge of an elytron and one mm long, ~60 % smaller than the notches Hall et al. tested. We see little evidence that the notching scheme we employed negatively affected reproduction. Starting in 2011, along with elytral notching, we glued a flattened bee tag (http://www.beeworks.com) with a unique number/color combination to each ABB to track individuals across time and space. Butler et al. (2012) found that bee tags did not

adversely affect beetle survival. Depending on conditions, we kept most adults in the lab for one or several nights in plastic containers with damp paper towel while providing mealworms ad libitum, then released them through provisioning on a subsequent day. While we strove to keep them for as little time as possible, we did not release beetles during excessively cold or windy days to avoid unnecessary mortality.

Beginning in 2011, we halted trapping earlier than in previous years because we were no longer provisioning all captured beetles and wanted to reduce the amount of time our traps were competing with any natural carrion for the attention of reproductive adults. In 2013–2016, we trapped until we had enough beetles to provision 25 broods or until we neared the end of June, which is approaching the end of the ABB reproductive season on Nantucket.

Provisioning involved burying either a lone beetle (usually a male, 15–30 % of broods annually) or a male/female pair of beetles with a quail carcass (bobwhite: *Colinus virginianus*; average mass $\pm$ SD 2004–2006: 113 $\pm$ 15 g, 2007–2016: 139 $\pm$ 17 g) approximately 20 cm underground. We increased the size of the quail in 2007 in an attempt to increase brood size. To protect the carrion and beetles from scavengers, we stapled 6-mm mesh hardware cloth

to the ground over the burial chamber. Twelve days after provisioning, we randomly selected and checked between 25 and 35 % of the broods and recorded the number of larvae and their instar stage. We estimated larval production by multiplying the average successful brood size that year, the brood success rate and the total number of unchecked broods and added this value to the number of counted larvae from checked broods (Amaral et al. 1997). From 2004 to 2010 all captured beetles were provisioned either as a pair or individually. Starting in 2011, we reduced provisioning 75 % to 25 or fewer broods each year. The goal was to match the provisioning effort on Block Island, gather annual reproductive data, and ensure the continuation of the population while we monitored the effects of reduced provisioning.

We began trapping for newly emerging juveniles each summer ~52 days after provisioning, roughly a week before their predicted emergence at 60 days, in case of early emergences. We also briefly trapped each year well before the predicted emergences in an effort to detect ABBs reared on naturally found carrion. For newly emerged beetles, we followed the same measuring and tagging protocols as with reproductive adults, though all measurements and marking was done in the field rather than in the lab. We immediately released processed beetles. We estimated overwinter

Fig. 2 Population density of American burying beetles in the 64 km² trapping area on Nantucket Island (*black line*, primary axis) and the number of broods provisioned each year (secondary axis, *gray bars*)
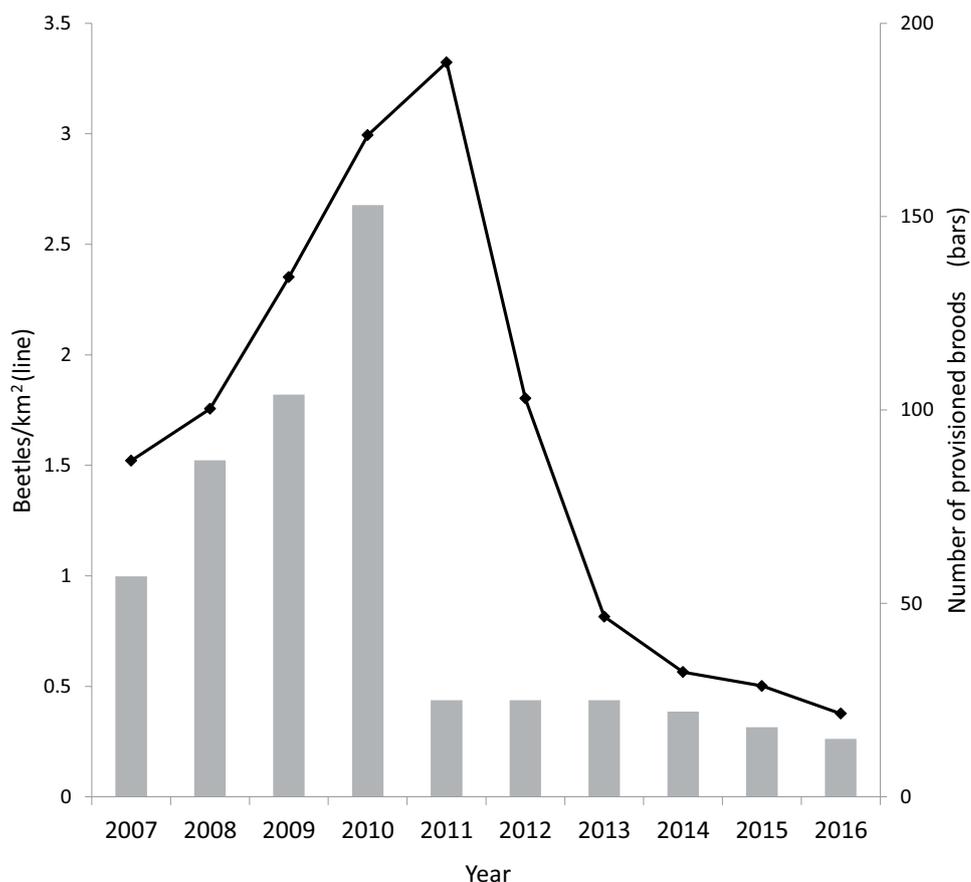
survival based on the proportion of these beetles captured in early-season trapping the following year.

Results

Overall

Adult (early-season) capture rates (number of beetles captured/number of trap nights) and density have fluctuated since 2004 (Table 1). However, until 2011, the number of wild beetles (i.e. not captive reared and released) consistently increased each year and we saw the highest number of captures and highest density in 2011 (Fig. 2). After reducing

provisioning in 2011, the density has decreased each year. The number of ABBs captured each summer is significantly and positively correlated with the number of broods provisioned the previous year [linear regression, $R^2 = 0.85$, $F(1,7) = 39.7$, $p = 0.0004$]. Late summer trapping in 2014–2016 timed to catch ABBs reared in broods other than the ones we provisioned recovered no ABBs suggesting few if any were able to find and reproduce on naturally occurring carrion. Accumulation curves suggest that in most years we captured most of the available ABBs (Fig. 3). Curves reach an asymptote in all years except 2011, 2012 and 2015.

We captured other carrion beetles in the traps in varying numbers depending on location and time of year. Species included, *Nicrophorus orbicollis, N. tomentosus, N.*
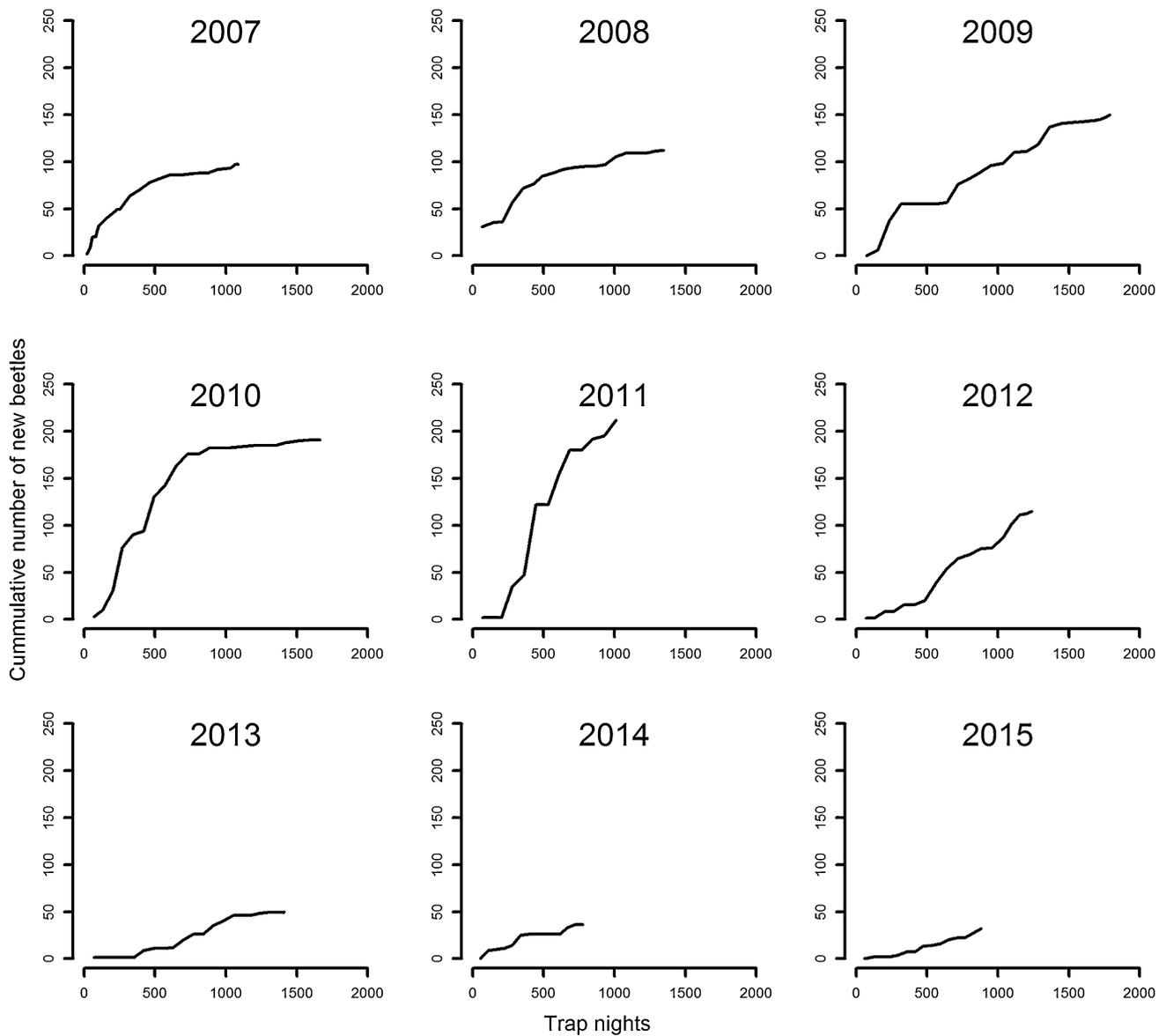
Fig. 3 Cumulative number of new American burying beetles versus trap night for each year through 2015 since trapping was expanded in 2007

marginatus, Necrodes surinamensis, Necrophila americana, Oiceptoma inaequale, and *Oiceptoma noveboracense*. The most commonly captured *Nicrophorus* species was *N. orbicollis* averaging about one beetle per trap night. This is about four times that of the peak ABB trap rate in 2011. The most common species overall was *Necrodes surinamensis* averaging 2–6 beetles per trap per night annually. Tracking the capture rates of these species helps us make inferences on general trapping conditions and the general characteristics of the carrion beetle community. Specifically, a site that captures these species at the same rate as other sites but does not catch ABBs is a good indicator that ABBs are not in the area.

Provisioning

Provisioning methods produced an estimated 8,089 larval beetles over 12 years and the success rate among broods was 54 % (Table 2). A significant increase in average successful brood size after 2007 correlates with an increase in quail mass [linear regression, $R^2 = 0.70$, $F(1,11) = 25.1$, $p = 0.0004$]. Of 1,080 provisioned broods, we excavated 428 (40 %). Of the excavated broods 197 (46 %) did not produce ABB larvae and on average 43 ± 18 % failed each year. Six percent of these failed broods were usurped by other carrion beetle species, including *Nicrophorus orbicollis* (67 %), *N. tomentosus* (29 %), or *N. marginatus* (4 %). Twenty-two percent of carcasses with no *Nicrophorus* larvae were populated by fly larvae or ants and the remaining 72 % were completely abandoned without obvious cause.

Overwinter survival

The overwinter survival rate is the ratio of the number of beetles captured in an early trapping season with elytral notches and/or a bee tag from the previous fall to the total number of beetles marked the previous fall. On average, we recovered 15 % of beetles marked the previous season (Table 3). This estimate is based on data from 2007 to 2016 when the trap area was much more comprehensive than 2004–2006. Data from the larger trap area should more

Table 3 The number of teneral beetles marked one year and recaptured the following year since 2007

Year of capture	Broods provisioned	Number marked previous year	Number captured	Percent recaptured
2007	57	82	12	15
2008	87	87	9	10
2009	104	112	21	19
2010	153	372	51	14
2011	25	434	63	15
2012	25	139	31	22
2013	25	77	15	20
2014	22	42	6	14
2015	18	35	3	9
2016	15	80	9	11
Overall	531	1460	220	15 ± 4

Table 2 Provisioning data and teneral beetle population estimates for all provisioning sites since 2004

Year	Total # broods	# broods checked	Avg. carrion mass (g)	# broods successful	% success	Avg. successful brood size	# larvae counted	# est. larvae	Total est. larvae
2004*	248	136	114 ± 21	73	54	11 ± 6	788	665	1453
2005*	238	91	115 ± 13	45	49	10 ± 5	448	720	1168
2006*	63	13	111 ± 14	10	77	10 ± 4	107	385	492
2007	57	16	133 ± 15	13	81	17 ± 7	200	565	765
2008	87	29	145 ± 29	14	48	15 ± 8	215	418	633
2009	104	37	139 ± 20	26	70	16 ± 7	416	750	1166
2010	153	58	138 ± 9	25	43	17 ± 7	445	694	1139
2011	25	8	135 ± 13	5	63	16 ± 5	82	171	253
2012	25	8	137 ± 14	5	63	21 ± 6	105	225	330
2013	25	10	142 ± 6	3	30	18 ± 5	53	81	134
2014	22	8	140 ± 11	4	50	12 ± 12	46	84	130
2015	18	7	151 ± 17	6	86	23 ± 3	140	218	358
2016	15	7	122 ± 9	2	29	16 ± 1	31	37	68
Overall	1080	428	133 ± 20	231	57 ± 18	14 ± 7	3076	5013	8089

Asterisks (*) indicate years when ABBs were reintroduced to the island from captive reared stock. Standard deviations are reported with averages. The percent success average is an average of yearly values, other averages are calculated using aggregated data from all years

accurately reflect actual survival within the range whereas data from isolated trap lines might only reflect survival by beetles that stayed near the trap lines.

ABB movement

Recaptured beetles in the early summer moved an average of 1.8 ± 1.0 km between captures. We recorded single-night movements of 3.9 km in 2011 and 3.8 km in 2012. Several beetles moved this distance in two or more nights, or moved back and forth between sites multiple times. In an extreme case in 2011, a beetle was captured 10.5 km away from its original capture site. Based on pooled data from 2011 to 2012 (years with the most complete and largest recapture dataset), 46 % of recaptured adult beetles were captured at least once at a different site than the one at which they were last seen.

Teneral beetles moved long distances between their original capture site in the late summer and their recapture site the following spring. Pooled data from 2012 to 2013 shows that only seven (21 %) of the 33 beetles recaptured after one winter were found at their initial capture site. Teneral ABBs moved an average of 3.0 ± 1.1 km between 2011 and 2012 and 2.1 ± 1.4 km between 2012 and 2013.

Bee tag retention

A majority of bee tags survived the winter and were readable the following summer. Pooled data from 2011 to 2013 shows that of the 46 beetles marked as tenerals and recaptured the following year, 34 (74 %) were readable, seven (15 %) were still glued in place but only partly readable, and five (11 %) were completely missing (beetles were identified to site using notched elytra). Bee tags also survived provisioning well. After provisioning in 2012, we recaptured 10 beetles and all except one (90 %) had readable tags. The color was still visible on the unreadable tag. This retention rate may be artificially high since provisioned beetles are released into a partially excavated chamber and would spend less time digging than if they found carrion naturally.

Discussion

Without human intervention, the Nantucket ABB population will probably disappear. The data show that we were able to increase the population through captive breeding and release but that this population is not self-sustaining. Bee tags and elytral notching allowed us to track ABB movement and adapt our trap site locations to maximize captures. Expanding the geographic spread of the trap sites and trapping over most of the reproductive season boosted the number of beetles captured allowing us to provision more

broods and produce more offspring. Increasing the carrion size in 2007 provided additional resources to increase brood size. Provisioning all of the captured beetles over successive years created stability in the growing population.

Several mechanisms may account for the observed decrease in beetle captures since 2011: an inability of wild ABBs to find available carrion, poor success in rearing young on carrion, low brood size, a drop in overwinter survival rates, competition for available natural carrion, or a lack of suitable natural carrion.

While our data do not specifically address all of these potential mechanisms, we can evaluate each in relation to the data we have. Ability to find carrion and a drop in overwinter survival rate are unlikely explanations. Beetles moved long distances with regularity during this study, especially between fall and early summer, suggesting that an ABB should be able to access available carrion and reproductive mates if present on Nantucket. Poor overwinter survival is not a likely explanation for the decrease in population because the calculated overwinter survival rates before and after the reduction in provisioning are not different (Table 3). Low reproduction success and low brood sizes are also not likely to be directly responsible for the dramatic decrease in population size. Before 2011 the population was increasing even with low brood sizes and low provisioning success in some years. While variations in these two parameters could drastically change the population size, they show no decreasing trend since 2011. There is evidence that our estimates for one or both of these parameters is conservative. In seven out of eight years since 2008, we captured more ABBs in the early summer than we would expect based on a 15 % winter survival rate.

Lack of carrion availability is the most likely factor in the decline of the Nantucket ABB population. Other studies suggest carrion availability is an important component for a self sustaining population (Arkansas and Oklahoma: Holloway and Schnell 1997; range-wide: Sikes and Raithel 2002). Historically, ABBs may have used the extinct passenger pigeon (*Ectopistes migratorius*) as a carrion resource on Nantucket (Brooks 1928) along with other bird species. Overall, North American grassland and shrubland bird species have declined steeply in the last 200 years (Hunter et al. 2001). It has been hypothesized that the introduced ring-necked pheasant (*Phasianus colchicus*) population on Block Island is a reason for the persistence of ABBs there (personal comm. Christopher Raithel). On Nantucket, the ring-necked pheasant is extremely rare and found in <0.01 % of birding lists (41/6,095); whereas on Block Island, it is far more common, found on nearly 21 % of lists (351/1,688) (1996–2016 eBird data, accessed 21 Sept 2016). Historic sources of carrion have been lost on Nantucket and suitable substitute species may not be abundant enough to maintain a self-sustaining population.

Competition for available carrion, while not explicitly evaluated by our work, is a possible compounding factor in the Nantucket ABB's decline since 2011. If carrion is available, ABBs may compete to locate and access it both with vertebrate scavengers and other carrion beetles (Sikes and Raithel 2002). Nantucket lacks typical North American mammalian scavengers like those DeVault et al. (2011) identified including the Virginia opossum (*Didelphis virginiana*) and raccoon (*Procyon lotor*). A pilot camera trap survey conducted by the authors and others in 2015 and 2016 on Nantucket captured white-tailed deer (*Odocoileus virginianus*), Norway rats (*Rattus norvegicus*), cats (*Felis catus*), dogs (*Canus lupus familiaris*), turkey vultures (*Cathartes aura*), American crows (*Corvus brachyrhynchos*), blue jays (*Cyanocitta cristata)*, American robins (*Turdus migratorius*), and northern harriers (*Circus cyaneus*) feeding at stations baited with a mouse or quail carcass (unpublished data). However, while ABB competition with vertebrate scavengers seems likely, its true impact has not been quantified and is an area for future study. Smaller carrion beetle species commonly found in our traps may also compete with the ABBs to find and defend a carcass. Fierce interspecific competition among *Nicrophorus* species is documented and there is evidence that body size positively correlates with the ability to fend off competitors suggesting the ABB should have an advantage (Wilson and Fudge 1984; Trumbo 1990). On Nantucket, *Nicrophorus tomentosus* and *N. orbicollis* were both found on excavated carcasses originally provisioned with ABB adults, though we believe that these beetles most likely took over the carcasses after the ABBs abandoned them. Both of these species are very abundant on Nantucket. With this consideration, speculating on how competitive ABBs are after locating a carcass is inconsequential if the sheer abundance of the other *Nicrophorus* species searching for carcasses give ABBs few chances to compete.

We conclude that a lack of available carrion compounded by competition is the most likely factor preventing a self-sustaining population of ABBs on Nantucket, but we can only speculate why ABBs remain in our trap area despite these impediments. Our results show that the relatively simple method of capturing ABBs and provisioning pairs or individuals with a carcass effectively negates inhibiting factors. However, we have also shown that Nantucket ABBs are good dispersers and that beetles move farthest between their capture in the late summer and their recapture the following spring. We question why they remain on the island between when we close traps in the late summer and open them again the following June. If there was no incentive for ABBs to remain on Nantucket (e.g. an abundance of carrion), it seems probable that they would leave our trap area and disperse widely in the spring in search of mates and carrion. As a possible explanation, we suggest that the island setting enhances the effectiveness of ABB trapping and may have played an important part in the success of our trapping methods year after year. While no work has been done on this topic, we hypothesize that the ocean may lack anything to attract dispersing ABBs (e.g. lights or carrion) creating a disincentive for the ABBs to take full advantage of their dispersal abilities. The resulting reduced emigration could explain the continued presence of ABBs each summer despite the assumed lack of reproductive resources.

Our hypothesis that a reduction in provisioning effort would lead to a decline in the population is supported and this provides the foundation necessary to considering future management goals for this population. An immediate question is what population density is appropriate for the island. Our methods dramatically increased the population and could conceivably maintain the population at any arbitrary density, but an appropriate target population density would be one that is comparable to natural populations. With no information on historical densities of the ABB population anywhere in its range and the lack of historic information on the preferred carrion for ABBs, it is difficult to identify a target density. There are numerous published surveys of current ABB populations (Creighton et al. 1993; Holloway and Schnell 1997; Carlton and Rothwein 1998; Backlund et al. 2008), but trapping methodologies differ so greatly and the lifecycle of the ABB is so resistant to population estimation techniques, it is difficult to identify target population densities for any given area. Carlton and Rothwein (1998) suggest that a trap rate (beetles per trap night) in the range 0.03–0.09 be considered an indication of an intermediate population and a trap rate of 0.1 an indicator of a robust population. Based on this scale, the Nantucket population reached robust levels in 2010 and 2011. However, for Nantucket, an area based metric may be more accurate since the island can be divided into distinct geographic areas. The best area data for natural populations come from Backlund et al. (2008), who explicitly estimated a June population of 442 ± 73 ABBs in a 220 km^2 area of South Dakota (2 ABB/km^2). This is equivalent to the Nantucket geographic density (ABBs/64 km^2) in 2009 and 2012 and slightly lower than the peak Nantucket density during the intervening years (~3 ABB/km^2) (Table 1; Fig. 2). Whether comparing data based on trap rates or beetles per area, our reintroduction and monitoring methodology fostered a population density on Nantucket that is comparable to western populations that are considered robust. Currently, there is no indication that the eastern and western ABB populations are significantly different in physiology, morphology, or lifecycle. With this consideration, we suggest that two ABBs per km^2 or a trap rate of 0.1 may be a good goal for this and other ABB reintroduction programs.

The future of ABBs on Nantucket Island is uncertain but we have shown that it is dependent on human intervention and will most likely not be self-sustaining at detectable levels. The

project has also identified comparison markers for ABB density, dispersal, and reproduction with which to evaluate future success and defined the resources needed to increase abundance and maintain the species existence. Our understanding of how provisioning and trapping affect the Nantucket ABB population provides the opportunity to fully utilize the designation of this species on Nantucket as an experimental population to inform ABB management range-wide.

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