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ORIGINAL PAPER

Population trends and flight behavior of the American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae), on Block Island, RI

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Abstract The endangered American burying beetle, *Nicrophorus americanus*, was monitored on Block Island, RI, USA, from 1991–2003 using mark-recapture population estimates of adults collected in pitfall traps. Populations increased through time, especially after 1994 when a program was initiated that provided carrion for beetle production. Beetle captures increased with increasing temperature and dew point, and decreased with increasing wind speed. Short distance movement was not related to wind direction, while longer distance flights tended to be downwind. Although many individuals flew considerable distances along transects, most recaptures were in traps near the point of release. These behaviors probably have counterbalancing effects on population estimates.

Keywords American burying beetle · Endangered species · Flight behavior · Mark recapture · *Nicrophorus americanus* · Population trends

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Introduction

The American burying beetle (*Nicrophorus americanus* Olivier) has declined profoundly throughout its natural range, and was listed in 1989 as an Endangered Species by the U.S. Fish and Wildlife Service (Federal Register 1989; vol. 54, no. 133). There were only two known populations in 1989: one on Block Island, Rhode Island and one in southeastern Oklahoma near Red Oak. Other western populations have since been discovered and *N. americanus* is now locally distributed in Oklahoma, Arkansas, Kansas, Nebraska, and South Dakota. Additional populations have not been discovered in the eastern portion of its range, but reintroductions have been attempted at Penikese Island and Nantucket Island, Massachusetts.

Population monitoring is a crucial element in conservation programs for this species. The Rhode Island Department of Environmental Management has monitored the population on Block Island since 1991, using a combination of pitfall trapping of adults and mark-recapture estimation of population numbers (Raithel 2002). Population estimators require assumptions about the equal availability of animals to recapture and adequate mixing of marked individuals prior to the recapture interval (Southwood 1978). Although these assumptions are critical to the valid interpretation of population estimates, they have only rarely been evaluated empirically.

In this paper, we present the results of 13 years of monitoring data for the Block Island population of *N. americanus*, and we use the capture histories of uniquely marked individuals to assess beetle movement patterns, including the direction of beetle movements relative to the prevailing wind direction, and the effects of weather on beetle activity. We then ascertain whether beetle flight behavior results in departures from the assumptions of mark-recapture analyses, and discuss the implications for population monitoring. There have been no published studies to date evaluating trapping bias and mark-recapture assumptions of pitfall trapping surveys for this species.

Methods

The Block Island population has been monitored annually since 1991 with standardized survey methodology developed by Kozol (1991). The annual survey involves three consecutive nights of pitfall trapping during the third week of June. This was an attempt to sample at roughly the same time in beetle phenology each year. Yearly differences in phenology might have affected assessments of population size in any given year, but should not affect assessments of trends through time over a 13-year period. Pitfall traps consist of 1-liter wide mouth glass jars sunk into the ground so that the lip is flush with the surface. Each trap is baited with a plastic screen-top jar containing about 10 g of aged (10-days) chicken. Fifty baited pitfall traps are placed 20 paces apart, arranged in three linear transects in southwest Block Island, for a total sampling effort of 150 trap-nights. Traps are shielded with rain lids to prevent flooding and damp sponges are placed in the traps to provide water (Bedick et al. 1999). Traps are left open during the daytime but are moved slightly if *Lasius niger* ants appear. From 1991 to 2001 beetles were given identification marks to delineate capture site by notching in locations along the posterior margins of elytra. Since 2002, numbered tags have been affixed to elytra. These unique tags allow a more detailed capture history for each animal. Animals are sexed, marked and released near their capture point. The release point is recorded for each captured beetle.

Kozol (1991) originally analyzed one year's mark-recapture data with two statistical methods: Lincoln–Petersen Index and Sequential Bayes Algorithm. Since 1992 the primary population estimator has been the Lincoln–Petersen Index with a Bailey correction for small sample sizes (Bailey 1951). Typically, Lincoln–Petersen estimates are calculated between day 1 and day 2 of trapping and again between day 2 and day 3 with the entire pool (day 1 and day 2) of marked animals.

Activity patterns were assessed within years by standardizing each day's captures by dividing the number of daily captures by the mean for the three sample days that year. This approach avoided the possibly confounding effects of year-to-year changes in beetle numbers. Weather data were recorded at the Block Island airport (National Climatic Data Center 2003), which is in the vicinity of the sample site. Readings of temperature, dewpoint, and wind speed for the period of greatest beetle activity (from 9:30 PM through midnight each day) were standardized in the same way as the beetle capture data. Thus, beetle activity was compared to weather variables standardized within each year.

The effects of weather variables on beetle activity were analyzed by stepwise multiple regression, trends in beetle populations through time by linear regression, and influence of wind on direction of beetle movement using Fisher Exact Probability tests, all using the BIOMstat statistical package (Rohlf and Slice 1999).

Results

Population trends

Estimated population sizes for the *N. americanus* population on Block Island, RI, from 1991 to 2003 are shown in Fig. 1. Overall, the population has increased during that time period, with a significant positive regression of the number of beetles on sample year ($F = 5.8536$, $df = 1, 11$, $P = 0.034$). The beetles were provisioned with carrion starting in 1994, with the number of carcasses varying each year, averaging about 36 per year. Methods used on Block Island to provision carrion were similar to those employed on Penikese Island (Amaral et al. 1997). There was no population trend from 1991 through 1994 ($F = 0.2297$. $df = 1, 2$, $P = 0.679$), but the population increased through time after 1994 ($F = 17.3915$. $df = 1, 7$, $P = 0.0042$). The ratios of the number of beetles each year (mean of the estimates) divided by the number in the previous year are shown in Fig. 2. Population estimates increased relative to the previous year in some years and declined relative to the previous year in others, with no obvious trend through time.

Activity and movement patterns

Results of a stepwise multiple regression using the standardized weather variables to predict standardized captures are shown in Table 1. Temperature, dewpoint and wind speed all added significantly to the regression equation, showing that all three of these factors influenced beetle activity ($F = 7.7955$, $df = 3, 20$, $P = 0.0013$). Activity was positively related to temperature and dewpoint (related to water content in the air), and negatively related to wind speed (Table 1).

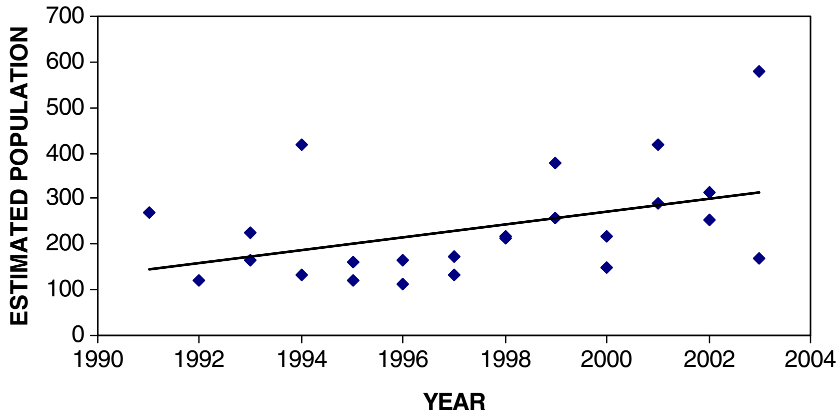


Fig. 1 Mark-recapture population estimates for *Nicrophorus americanus* on Block Island, RI, from 1991–2003

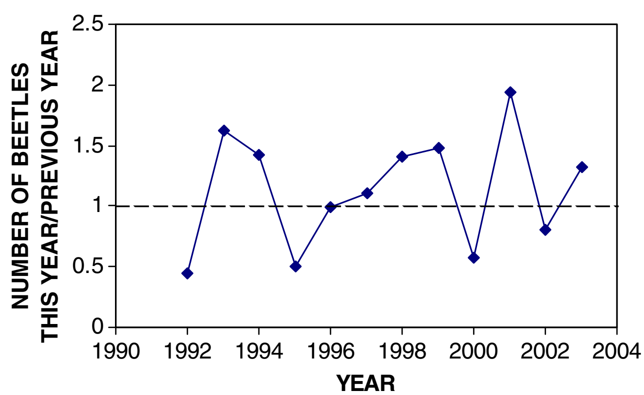


Fig. 2 Mean population estimate each year divided by the previous year's mean population estimate

Table 1 Multiple regression of standardized beetle activity on standardized weather variables

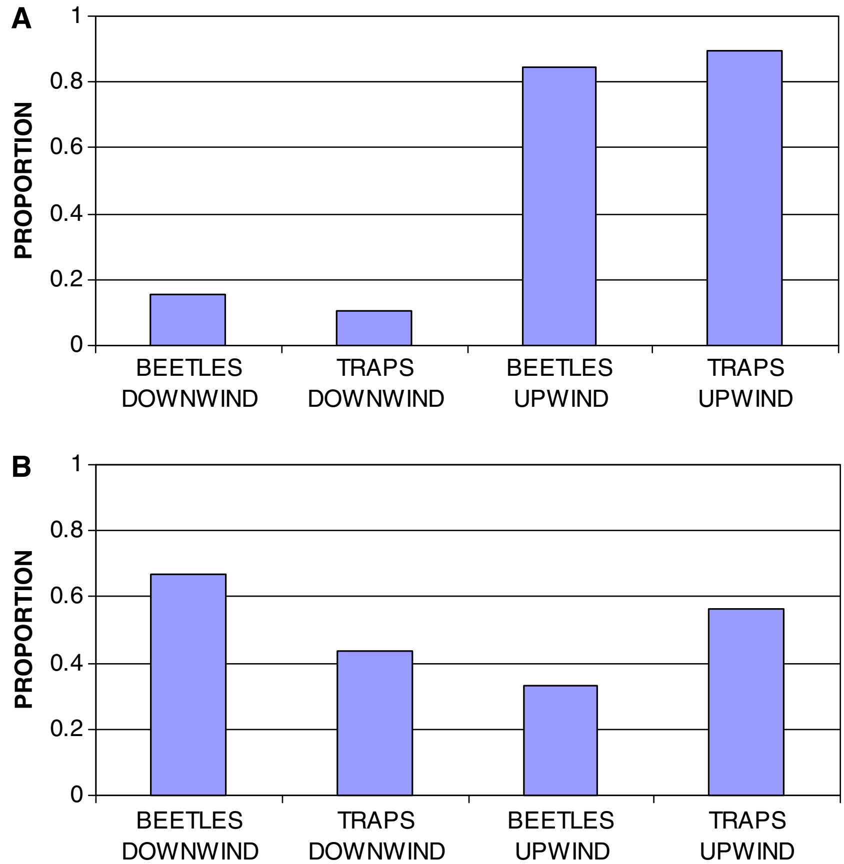
Variable	Coefficient	*t*	*P* (2-tailed)
Constant	–9.8003	–3.9128	0.00086
Temperature	7.6859	4.1086	0.00055
Dewpoint	4.1837	2.6653	0.01486
Wind speed	–1.0611	–4.0167	0.00068

The influence of wind on the direction of movement after release of marked individuals was assessed by comparing the number of moves with versus against the wind to the number of traps in each direction (Fig. 3). For traps within individual transects, the proportion of moves with versus against the wind did not differ significantly from the proportion of traps in those directions (Fisher Exact Probability Test, $P = 0.141$). Therefore, for short-range flight beetles flew without regard to wind direction (Fig. 3A). In contrast, when beetles were captured on different transects from where they were released, the proportion of recaptures in the downwind direction was greater than the proportion of traps in that direction (Fisher Exact Probability Test, $P = 0.035$), so for longer distance flights beetles tended to fly downwind (Fig. 3B).

Flight distance, reported as the number of traps from release to recapture, is shown in Fig. 4. More than a third of the recaptured beetles (36.9%) were captured more than five traps away from the release point (Fig. 4A). However, about one third of the beetles (32.6%) were captured at the same trap or within two traps of release. In terms of distance flown relative to the distance to the farthest trap along the transect, 21.7% of the recaptures were over three quarters of that distance, while 50% of the recaptures were within one quarter of the distance to the farthest trap.

The actual number recaptured per trap (Fig. 4A) does not present an accurate picture of beetle dispersion, because beetles fly in all directions from the release point, so more distant traps sample from a larger area than traps near the release point. To correct for this problem, a line was fitted to the numbers

Fig. 3 Relationship of beetle movements to wind direction: number of beetle recaptures and number of traps upwind and downwind from release points (**A**) Within transects. (**B**) Between transects



of beetles captured at each distance, adjusted for the area sampled by each trap (Fig. 4B). Despite the zeroes in several traps at greater distances (because there were fewer traps per unit area than at distances closer to the release point), it is clear that considerable numbers of beetles flew hundreds of meters from the point of release during the few days of sampling.

Discussion

The *N. americanus* population on Block Island, RI, displayed a generally increasing trend from 1991 to 2003 (Fig. 1). The fact that the population trend was flat from 1991 to 1994, but then increased substantially after 1994 when carrion was provided, suggests that availability of carrion limited beetle populations. However, because of the small number of years before carrion was provided, and the lack of replication or appropriate controls, this interpretation remains tentative.

Despite the increasing trend in the *N. americanus* population in recent years, numbers fluctuated considerably from year-to-year, including declines in mean estimates from previous years in 2000 and 2002 (Fig. 2). We were unable to correlate these fluctuations with weather variables or with population estimates of potential carrion species. Nevertheless, the clear overall increase after provision of carrion is compatible, at least, with the ‘‘loss of ideal carrion’’ hypothesis (Sikes and Raithel 2002) for the long term decline of this species.

Beetle captures were clearly influenced by weather, increasing with temperature and dewpoint, and declining with increasing wind speed (Table 1). These results suggest that beetle activity increases with increasing temperature and humidity, and declines when the wind picks up. However, high winds might affect the ability of beetles to detect and enter baited traps, rather than affecting activity *per se*.

Wind direction did not affect movement direction for short distance (within transect) moves. However, longer distance moves (between transects) tended to be downwind (Fig. 3). This behavior would lower the number of recaptures if marked beetles left the sample area downwind, while unmarked individuals entered across the upwind border. Artificially lowered recapture rates would result in overestimates of the beetle population size. Unfortunately, without reliable estimates of the magnitude of downwind movement in and out of the population relative to population size, it

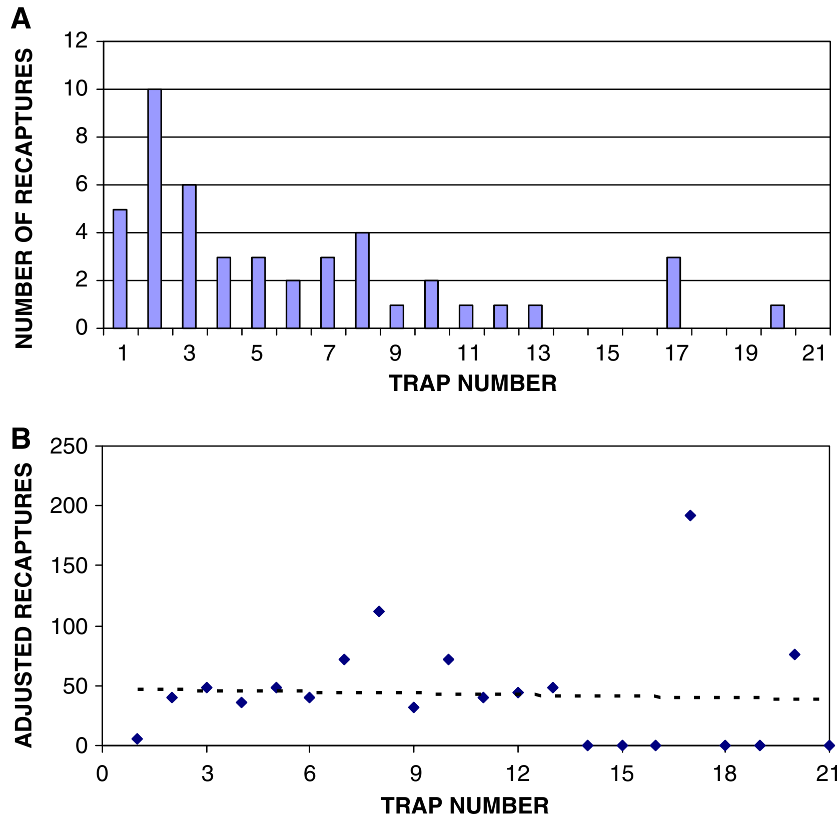


Fig. 4 Number of beetles recaptured in traps along transects, 2001–2003. Trap 1 is at release point. (**A**) Number of recaptures. (**B**) Estimated number, adjusted for area sampled by trap

is not possible to quantify the effects of this behavior on population estimates.

This potential overestimation of population size is balanced somewhat by the tendency of beetles to be recaptured at the release site, or within one or two traps distant (Fig. 4). The considerable distances flown by many beetles (Fig. 4B) suggest that marked beetles are reasonably well mixed in the population. However, traps are effectively more concentrated near release points so marked and released beetles are generally captured in greatest numbers near the release point, and they are more likely to be captured than random individuals in the population. This effect would tend to increase the number of recaptures. Artificially high recapture rates would result in underestimates of population size, and thus would counterbalance, to some degree, the effects of downwind flights on population estimates. In any case, there is no reason to think that the effects of downwind flights or of recaptures near the release point would shift in a systematic way through time, so their effects on population estimates probably do not affect our assessment of population trends during the thirteen year sampling period.

Our results provide no clear indication about the potential long-term viability of the *N. americanus* population on Block Island, if left alone. However, the increasing numbers in recent years argues for the utility of carrion provisioning as a maintenance tool for this population.

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