Use of track tubes to detect changes in abundance of beach mice

Author(s): Elliot B. Wilkinson, Lyn C. Branch, Deborah L. Miller, and Jeffery A. Gore

Source: Journal of Mammalogy, 93(3):791-798. 2012.

Published By: American Society of Mammalogists
DOI: http://dx.doi.org/10.1644/11-MAMM-A-251.5
URL: http://www.bioone.org/doi/full/10.1644/11-MAMM-A-251.5

Journal of Mammalogy, 93(3):791–798, 2012

Use of track tubes to detect changes in abundance of beach mice

Elliot B. Wilkinson,* Lyn C. Branch, Deborah L. Miller, and Jeffery A. Gore

Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611-0430, USA (EBW, LCB)
Department of Wildlife Ecology and Conservation, University of Florida, West Florida Research and Education Center, Milton, FL 32583-1713, USA (DLM)
Florida Fish and Wildlife Conservation Commission, 3911 Highway 2321, Panama City, FL 32409, USA (JAG)

** Correspondent: ebwilkinson@yahoo.com*

Track tubes may help measure impacts of disturbances on small mammals by providing information about the magnitude and timing of fluctuations in relative abundance. We evaluated live-capture and track-tube data from 8 trapping grids to test the utility of track tubes for monitoring abundance of beach mice (*Peromyscus polionotus*) through time and for comparing relative abundance of beach mice among sites. When averaged across grid sites, track indexes and abundance estimates exhibited strong covariation through time. Associations between the track index and estimated abundance on different grids varied from strong to very poor depending on sample period. Associations between track indexes and abundance estimates were strong when mouse densities on all grids were relatively low, but they were weak during other sample periods when densities were highly variable among grids. This study points to the need to understand factors that influence the relationship between indexes from track tubes and mouse abundance before track tubes can be used to compare abundances among sites.

Key words: abundance monitoring, beach mice, coastal habitat, *Peromyscus polionotus leucocephalus*, track tube

DOI: 10.1644/11-MAMM-A-251.5

Beach mice (*Peromyscus polionotus*) depend on coastal dune habitat in Alabama and Florida for burrow sites and other resources, making them vulnerable to natural and anthropogenic disturbances that are common to southeastern coastlines (Blair 1951; Oli et al. 2001; Pries et al. 2009; Swilling et al. 1998). Recent hurricanes have contributed to a decline in vegetation, elevation, and topographic relief within coastal dune habitat (Houser et al. 2008; Pries et al. 2008). Housing development also has destroyed coastal dune habitat, isolated beach mouse subpopulations, and supported invasive predators (Fedriani et al. 2001; Gore and Schaefer 1993). Monitoring populations of beach mice exposed to these disturbances is important, because 6 of 7 subspecies of beach mice are either threatened or endangered (Oli et al. 2001; Pries et al. 2009).

The use of mark–recapture techniques to monitor populations is a key part of wildlife management but often is hampered by cost, effort involved, and concern that sampling may negatively affect target populations (Kaufman and Kaufman 1994; Suazo et al. 2005). Recent studies have examined the utility of track tubes for population monitoring. These tubes are composed of baited polyvinyl chloride pipe with inked pads inside to record tracks of small mammals (Glennon et al. 2002; Mabee 1998; Wiewel et al. 2007). Previous studies have demonstrated that track tubes are inexpensive, easy to monitor, and pose no risk to animals (Drennan et al. 1998; Glennon et al. 2002; Loggins et al. 2010; Mabee 1998; Pries et al. 2009; Wiewel et al. 2007).

The number of track tubes that are visited within a specified amount of time at a study site can be used to create a track index, which is often positively associated with estimated abundance at that site (Drennan et al. 1998; Glennon et al. 2002; Mabee 1998; Wiewel et al. 2007). The strength of the relationship between track-tube indexes and abundance estimates may vary through time, but studies documenting this phenomenon have focused mainly on differences between years (Drennan et al. 1998; Wiewel et al. 2007). Determining whether the relationship between track-tube indexes and abundance estimates differs over smaller timescales is important given that population dynamics of small mammals often fluctuate dramatically over a single annual cycle (Leirs et al. 1997; Lima et al. 2003; Turchin and Ostfeld 1997).

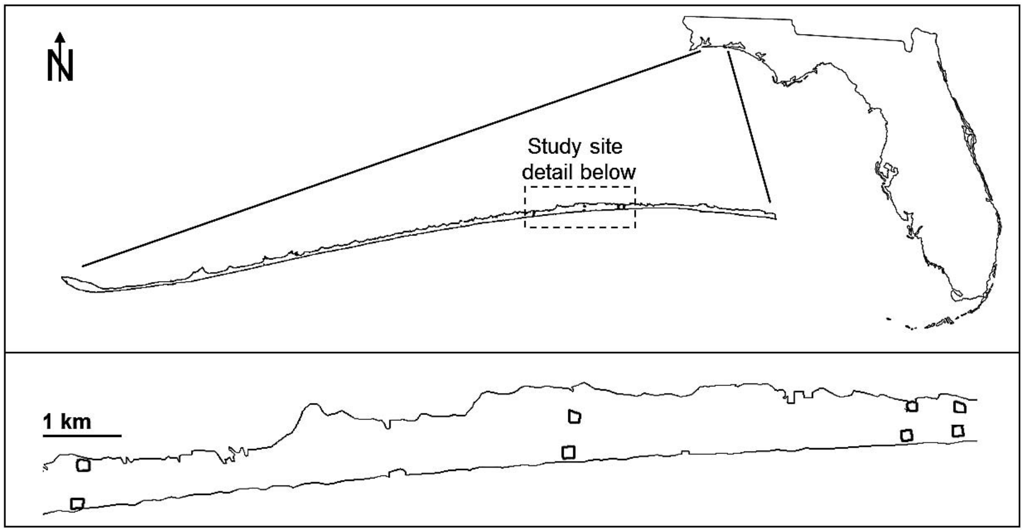


FIG. 1.—Map of the study site on Santa Rosa Island, Florida, indicating grid locations used to study the Santa Rosa beach mouse (*Peromyscus polionotus leucocephalus*) from 2007 to 2008.

Effective management decisions require an understanding of how populations of beach mice respond to the intense and repeated disturbance found along southeastern coastlines. This understanding may be facilitated by monitoring mouse populations through time and comparing their population trends before and after disturbances. When abundance data are not available from prior to a disturbance, the decision-making process may benefit from comparisons among sites that differ substantially in the level of disturbance they experience (space-for-time substitution—Michener 1997). In this study, we evaluate the utility of track tubes for monitoring changes in the abundance of beach mice through time. We also investigate whether track tubes can be used to compare relative abundance across sites by measuring the association between track indexes and abundance estimates at sites spanning a range of hurricane damage. We conducted our monitoring 4 times a year, thus incorporating seasonal changes in mouse populations that have not been the focus of previous evaluations of track tubes.

MATERIALS AND METHODS

Study system.—Beach mice are subspecies of the oldfield mouse (*Peromyscus polionotus*) that are unique to the coastal landscapes of Florida and Alabama (Van Zant and Wooten 2003). This study focuses on the Santa Rosa beach mouse (*P. p. leucocephalus*), which is the only subspecies of beach mouse not listed as threatened or endangered by the United States Fish and Wildlife Service (Gore and Schaefer 1993; Oli et al. 2001; Swilling et al. 1998). However, habitat requirements, degree of genetic relatedness, and threats to persistence are similar for the Santa Rosa beach mouse and other subspecies of beach mice in Florida and Alabama (Blair 1951; Oli et al. 2001; Van Zant and Wooten 2003).

Our study was conducted on Santa Rosa Island, a barrier island in northwestern Florida, in an undeveloped section of the island managed by Eglin Air Force Base (Fig. 1). Study sites were characterized by a mosaic of open, sandy interdune areas, sand flats with incipient dunes, and grassy, mixed grassy–woody, or woody scrub dunes near the Gulf of Mexico (Gulf side) or farther north toward Santa Rosa Sound (sound side; Fig. 1). This island has been damaged extensively by storm surge from hurricanes Opal (1995), Georges (1998), Ivan (2004), and Dennis (2005), resulting in erosion of prestorm dune area ranging from 15% of the dunes on the sound side to 68% of the dunes on the Gulf side (Pries et al. 2009). The proportion of our study sites covered by dunes that survived recent hurricanes ranged from 0.05 to 0.79 ($\bar{X}$ = 0.33, as quantified from geographic information system maps of remnant dunes created by Pries et al. [2009]).

Experimental design.—We compared mouse abundance and use of track tubes on 8 trapping grids, with 4 grids on the Gulf side and 4 grids on the sound side of Santa Rosa Island (Fig. 1). Grids were separated by a minimum of 153 m, which was more than 6 times the median nightly foraging distance of *P. p. leucocephalus* determined from a separate radiotelemetry study (25 m). Most grids were separated by larger distances (Fig. 1). To estimate abundance, we trapped mice with Sherman live traps (~7 × 8-cm opening; H. B. Sherman Traps, Inc., Tallahassee, Florida) placed in 7 × 7 grids with 20-m spacing between each trap (49 traps in each grid). Traps were set before sunset and left open for approximately 4 h. Each trap was baited with whole oats and contained polyester batting for insulation when nighttime temperatures dropped below 16°C. Captured mice were marked with an ear tag (1005 Monel tags; National Band and Tag Company, Newport, Kentucky) and released. Traps were set for 4–6 nights between last and 1st moon quarter in November 2007, March 2008, June 2008, and September 2008. Trapping in November 2007 was limited to the 6 grids installed by this date (3 Gulf side and 3 sound side), each of which was trapped for 6 days. In all other periods we trapped 8 grids for 4 days each.

Trapping procedures followed guidelines set by the American Society of Mammalogists (Sikes et al. 2011) and the University of Florida Institutional Animal Care and Use Committee (approved IACUC protocol A618-2007) and protocols established by the United States Fish and Wildlife Service (D. LeBlanc, United States Fish and Wildlife Service, pers. comm.).

To investigate relationships between track-tube indexes and abundance, we placed track tubes at the 49 sample locations in each grid. Track tubes consisted of 3.8-cm polyvinyl chloride pipe, capped at the end and open with a 90° elbow at the other to inhibit windblown sand (Loggins et al. 2010). A 5.1 × 27.9-cm paper liner with felt at the end was inserted into tubes, with the felt at the end nearest the tube opening. A 1:2 mixture of carbon lampblack and mineral oil was applied to the felt as ink, and whole oats were placed as bait at the back (closed) end of the tube. Tubes were suspended above the sand with 9 gauge wire stilts to prevent access by ghost crabs (*Ocypode quadrata*—Pries et al. 2009), and mice accessed the tube by climbing a dowel placed at the entrance. Mice traveled across the felt ink pad to retrieve bait, leaving tracks.

We trapped for 6 days in November 2007 and 4 days in March, June, and September 2008. We conducted trapping on half of all Gulf-side and sound-side grids while monitoring track tubes on the other grids, and then reversed this pattern. The order of trapping and track-tube efforts at grid sites was chosen randomly for each sampling period. Tubes were checked for tracks each day for the duration of each trapping period. Track tubes were left in place between sampling periods but were unbaited and closed to discourage use by mice.

Peromyscus polionotus leucocephalus may coexist with cotton rats (*Sigmodon hispidus*), cotton mice (*P. gossypinus*), and house mice (*Mus musculus*) on Santa Rosa Island. However, only house mice and cotton mice tracks are similar to those of beach mice. During the 6,468 trap nights conducted for this study, we captured 315 beach mice (839 total captures) and no cotton mice or house mice. Cotton rats were captured a total of 9 times, but their tracks are distinctly larger and have different morphology than those of beach mice. Thus, we are confident that tracks we recorded are from beach mice.

Analysis.—Abundance estimates from livetrapping at each grid site were obtained with program CAPTURE in MARK (M_h jackknife estimator—White and Burnham 1999). We used the M_h jackknife estimator because it produces estimates with low bias under conditions in which there is heterogeneity in capture probability between individuals (as is almost always the case—Stanley and Burnham 1998). We used the program CloseTest (Stanley and Richards 2005) to test whether the assumption of closure was met for each jackknife abundance estimate (closure test of Stanley and Burnham [1999]). The assumption of closure was violated for 1 grid during the March 2008 sample period ($\chi^2 = 9.87$, $P < 0.05$) and 1 grid during the June 2008 sample period ($\chi^2 = 14.12$, $P < 0.05$). We tested whether estimates from these grids might have biased the relationships between track indexes and estimated abundance by removing them from the analyses below. During the November 2007 sample period, abundance for 3 of the 6 grids could not be estimated with program CAPTURE because they did not contain sufficient recaptures. In these cases, we used the number of individuals known to be alive as abundance estimates.

We quantified whether abundance estimates from trapping grids exhibited positive spatial autocorrelation in order to identify whether lack of independence between trapping grids might affect our analysis. For each of the 4 trapping periods, we assigned the spatial location of each trapping grid centroid to the estimated abundance in that grid (M_h). We then used the Excel add-in ROOKCASE to compute spatial autocorrelation values (Moran's I) for abundance estimates at different lag distances (Sawada 1999). We used a lag distance of 400 m to ensure that at least 2 neighbor pairs were incorporated in Moran's I values for each lag distance. For all trapping periods we found no evidence for positive spatial autocorrelation in abundance estimates at any lag distance ($P > 0.05$ in all cases).

For each sampling period, we calculated a track index for each grid by summing the number of tubes that had tracks at the end of the sample period. Although we checked the tubes for tracks each day during sampling periods, we found that the number of days over which the track index was calculated did not affect the relationship between the track index and estimates of abundance from trapping in any consistent way (Appendix I). For consistency in our analysis, we used track indexes calculated over the same interval as abundance estimates (4–6 days, depending on sample period length).

To test the utility of track tubes for monitoring abundance through time, we calculated the serial cross-correlation between average track indexes and estimated abundance for all grid sites in successive sampling periods (R Development Core Team 2008). Cross-correlation involves shifting a data series forward or back in time with respect to another data series, a process known as lagging (Legendre and Legendre 1998). The correlation of data series exhibiting similar linear temporal trends but little covariation will be insensitive to lagging a data series with respect to the another data series. In contrast, the correlation between data series exhibiting strong cyclic covariation should be sensitive to lagging each with respect to the other, especially if a temporal trend does not exist or has been removed prior to analysis. Cross-correlation analysis is especially useful for measuring temporal covariation of cyclic phenomena, as is commonly the case for small-mammal population dynamics (Leirs et al. 1997; Lima et al. 2003; Turchin and Ostfeld 1997). To test whether abundance estimates from grids that did not meet the closure assumption might have biased the relationship between average track indexes and estimated abundance, we removed the 2 grids that did not meet closure assumptions and recalculated the serial cross-correlation between average track indexes and estimated abundance for successive sampling periods. In addition, we tested whether our results were robust to the type of abundance estimator used by examining the serial cross-correlation between average track indexes and average minimum number of individuals known to be alive (MKA) for successive sample periods.

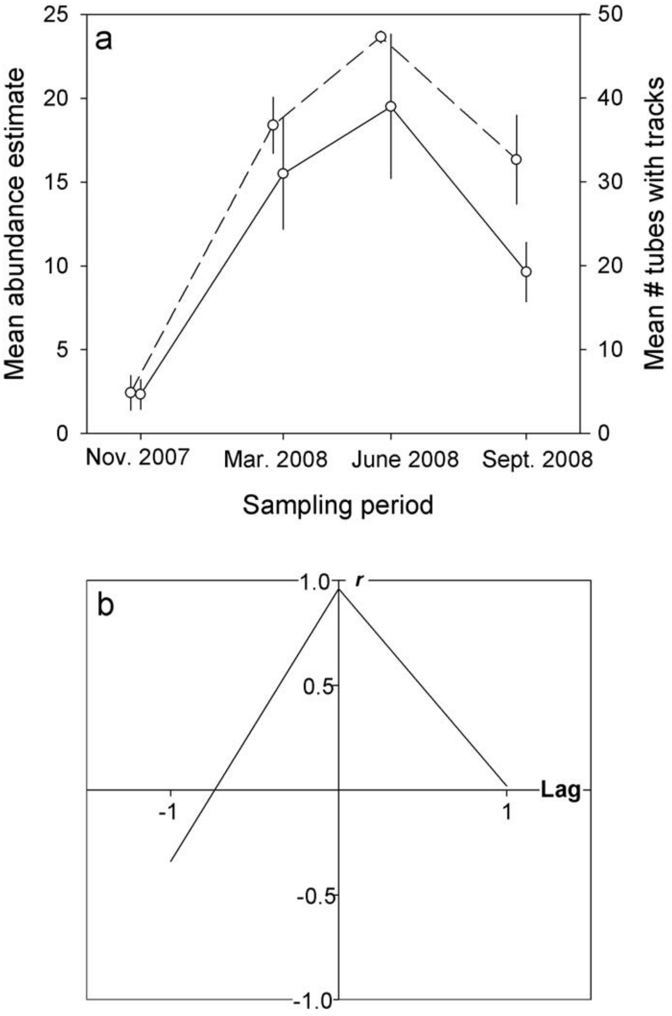


Fig. 2.—a) Variation in average number of tubes with tracks (dashed lines ± *SE*) and estimated abundance (M_h jackknife estimator; solid lines ± *SE*) of *Peromyscus polionotus leucocephalus* on Santa Rosa Island, Florida, during sampling periods from 2007 to 2008, and b) cross-correlogram depicting covariation (Pearson's *r*) between the 2 time series at different lag intervals (see ''Materials and Methods'' for details). Strong covariation at lag 0 and weak covariation at lag −1 and +1 indicate that track indexes and abundance estimates covary in phase with each other through time.

To test whether track tubes can be used to compare relative abundance across sites with differing amounts of hurricane damage, we examined the correlation between track indexes and abundance estimates at the sample grid sites (Pearson *r*—R Development Core Team 2008). We repeated this analysis for each sampling period and compared patterns of association among periods. To test whether abundance estimates from grids that did not meet the closure assumption (1 grid in March 2008 and 1 grid in June 2008) might have biased the relationship between track indexes and estimated abundance during these sample periods, we recalculated the correlation between track indexes and estimated abundance, removing the 2 grids that did not meet closure assumptions. To determine whether the strength of correlations depended on the abundance estimator used, we also examined the correlation between track indexes and the MKA at the sample grid sites.

RESULTS

Monitoring abundance through time with track tubes.—Average track indexes exhibited strong covariation with average estimated abundance across seasons (Fig. 2a), as well as with average MKA across seasons. Covariation was strongest at lag distance 0 (Fig. 2b; M_h: $r = 0.96$, $P < 0.01$, MKA: $r = 0.97$, $P < 0.01$) but dropped precipitously at lag distances −1 (M_h: $r = -0.34$, $P > 0.05$, MKA: $r = -0.11$, $P > 0.05$) and +1 (M_h: $r = 0.02$, $P > 0.05$, MKA: $r = -0.09$, $P > 0.05$), which demonstrates that the average track index and estimated abundance (M_h or MKA) covary in phase with each other. Removal of the 2 grids that did not meet the assumption of closure did not change patterns of covariation between averaged track indexes and averaged jackknife (M_h) estimates of abundance (0 lag: $r = 0.97$, −1 lag: $r = -0.48$, +1 lag: $r = -0.04$).

Relationships between track indexes and abundance estimates on grids.—Relationships between track indexes and abundance estimates on grids did not depend on the method used to estimate abundance (M_h or MKA). The track index for each grid was positively correlated with estimated abundance (M_h) and MKA for that grid during November 2007 (M_h: $r = 0.86$, $P < 0.05$, MKA: $r = 0.83$, $P < 0.05$; Fig. 3a) and September 2008 (M_h: $r = 0.72$, $P < 0.05$, MKA: $r = 0.75$, $P < 0.05$; Fig. 3d) when abundance on all grids was relatively low. No association existed between the track index and estimated abundance during March 2008 (M_h: $r = 0.17$, $P > 0.05$, MKA: $r = -0.48$, $P > 0.05$; Fig. 3b) and June 2008 (M_h: $r = 0.27$, $P > 0.05$, MKA: $r = 0.29$, $P > 0.05$; Fig. 3c) sampling periods. Removal of the 2 grids that did not meet the assumption of closure did not change associations between track indexes and abundance estimates (data not shown in figure, M_h estimates for November 2007: $r = 0.86$, March 2008: $r = -0.18$, June 2008: $r = 0.07$, September 2008: $r = 0.72$). During the March and June 2008 sample periods average abundance for all 8 grid sites was relatively high (Fig. 2a), and abundance on individual grids was highly variable (Figs. 3b and 3c). During these periods mice visited most track tubes regardless of the estimated abundance at a grid site.

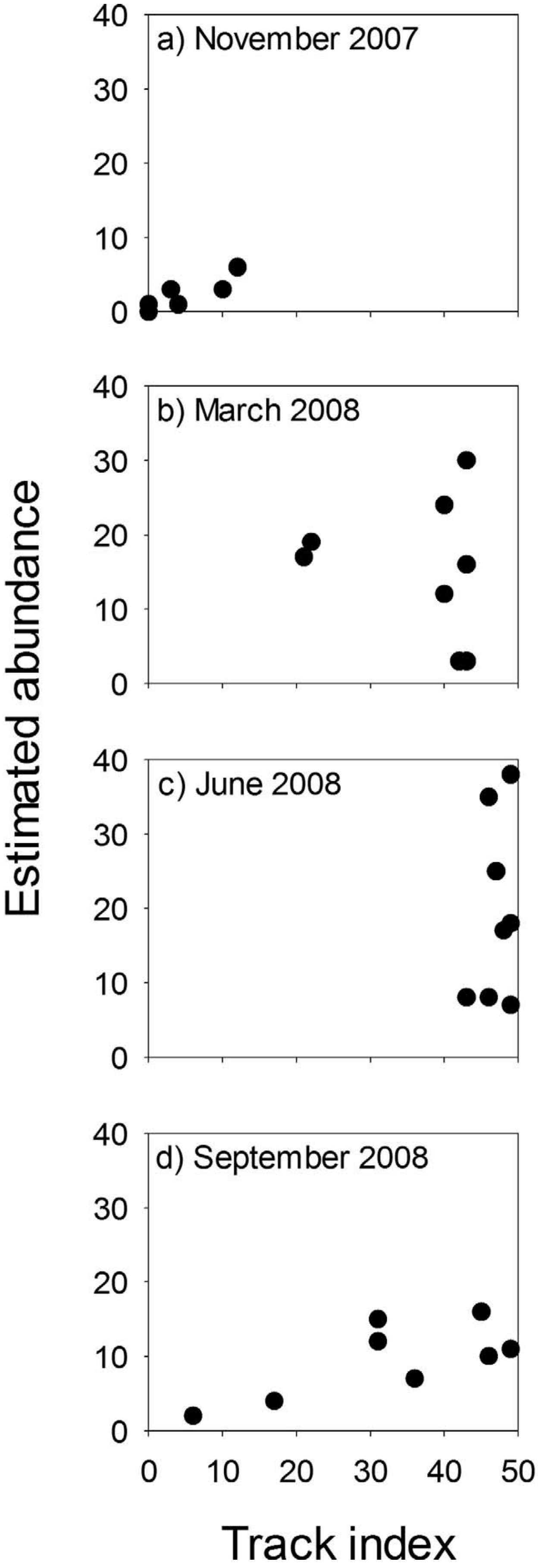
DISCUSSION

This study provides information on associations between track indexes and estimated abundance on a temporal scale that captures seasonal variation in populations, which has not been the focus of previous studies on track tubes (Glennon et al. 2002; Wiewel et al. 2007; but see Drennan et al. 1998). The strong covariation between average track indexes and abundance estimates across sample periods suggests that track tubes can be used to monitor large fluctuations in relative abundance over time. Patterns of covariation across time did not change when data from grids that did not meet closure assumptions were removed. Likewise, patterns of covariation did not depend on the type of estimator used (M_h or MKA). By providing information about the magnitude and timing of fluctuations in abundance, track tubes may help measure impacts of disturbances such as hurricanes and land development on beach mice.

Within a sample period, associations between the track index and estimated abundance on different grids varied from strong to very poor, depending on the sampling period. The pattern of association in different sample periods did not depend on whether data from grids that did not meet closure assumptions were removed, or on the methods used to estimate abundance (M_h or MKA). Thus, the results of this study are likely to be robust to type of estimator used and small differences in estimates between them (Stanley and Burnham 1998). The relationship between track indexes and abundance estimates were strong in September and November, corresponding to periods when estimates of abundance were low based on trapping. During March and June most tubes had tracks within 48 h after they were baited regardless of the estimated abundance on the grid, leading to weak associations between the track indexes and estimated abundance. Sites where estimates of abundance were low had similar numbers of tubes with tracks as sites with higher abundances.

Our results contrast with previous studies that observed smaller variations through time in the relationship between track indexes and estimated abundance (Drennan et al. 1998; Wiewel et al. 2007). In 1 instance, sampling occurred over much larger timescales and may have failed to capture seasonal variation (Wiewel et al. 2007). Although the sample interval of Drennan et al. (1998) was on a similar timescale as that in this study, the 2 sample periods encompassed a relatively stable portion of the annual population cycle of the focal species in comparison to the larger fluctuations in abundance observed in this study. The lack of correspondence between the number of tubes with tracks and estimated abundance could occur for several reasons.

First, the degree to which abundance estimates based on mark–recapture reflect real population abundance may vary through time and across sites because the proportion of the population that enters traps changes over time and space. For



←

Fig. 3.—Associations between the number of tubes with tracks (track index) and estimated abundance (M_h jackknife estimator) of *Peromyscus polionotus leucocephalus* at sample grid sites on Santa Rosa Island, Florida, for a) November 2007, b) March 2008, c) June 2008, and d) September 2008 based on 6 days of sampling for November 2007 and 4 days of sampling for other months. See Appendix I for cumulative track indexes for each day of sampling and the ''Materials and Methods'' for details concerning calculation of track indexes and estimated abundance. The data presented here include all grids because removing grids that did not meet the assumption of closure had little effect on associations between track indexes and estimated abundance (see ''Results'').

instance, some small mammals increase their propensity to enter traps during the breeding season, independent of the presence of food resources in traps (Daly et al. 1978). Others may exhibit spatial heterogeneity in trap response depending on local topography or vegetation (Huber 1962; Parmenter et al. 1998; Perry et al. 1977). If these patterns apply to beach mice, then the relationship between the track index and the estimate of abundance may be poor because mark–recapture data do not produce estimates of abundance that correspond to real population abundance. However, this explanation for the lack of concurrence between abundance estimates and track indexes assumes that factors affecting entry into track tubes are different from factors affecting entry into traps.

A 2nd, and perhaps more likely, explanation is that the rate of visitation of tubes varies over time and space as a function of environmental factors or the physiological state of the animals. The factors potentially influencing variation in the number of tubes visited per mouse were not investigated here, but they may include energetic demands for reproduction and growth during March and June, differences in food resources among sites, or interactions between these and other factors. Reproduction and population growth of *P. p. leucocephalus* peak during spring (Blair 1951), which is similar to other subspecies of beach mice (Swilling et al. 1998). Energetic costs associated with reproduction (deRivera 2003) and increased propensity to enter tubes during the breeding season (Daly et al. 1978) may lead to higher rates of tube visitation per individual. Likewise, an inability to meet energetic demands when population densities are high may lead to higher rates of tube visitation per individual (Prendergast et al. 2001). Such trends may be exacerbated at sites where resource availability is low due to hurricane damage because individuals may be more willing to enter tubes to retrieve resources (O'Connell 1989). Additional studies are needed to identify factors that influence the number of tubes visited per mouse and to develop sample designs for tracking tubes that provide estimates of abundance over the entire range of conditions at the study site.

Difficulties associated with using track tubes to compare relative abundance between sites potentially could be overcome through modifications of our sampling design. If differences in energetic state between individuals or between sample periods are likely, future studies may be able to dampen variation in the propensity to enter traps by leaving traps and track tubes unbaited. Other modifications might include checking tubes more often (>1 time per night if needed for greater precision—Nams and Gillis 2003) or employing an adaptive sampling period with a length that varies according to initial capture success. The use of a sample grid geometry that more closely mirrors the foraging range of the focal species also may alleviate some of the difficulties of comparing relative abundance using track tubes. The 20-m spacing employed in our sample geometry may have allowed a small number of mice to visit a large number of tubes, thereby lessening the sensitivity of the track index to differences in mouse abundance and also may have encouraged individuals to trapline tubes. However, increasing the distance between track tubes also decreases their density, which might reduce the sensitivity of the track index. Although track identification was not an issue in this study because of the simplicity of the small mammal community on Santa Rosa Island, other studies incorporating track tubes are likely to focus on more diverse communities. Developing a comprehensive and accurate library of tracks associated with each species (e.g., Drennan et al. 1998) will be a crucial 1st step in estimating abundance with track tubes.

Strengths associated with track tubes, such as low cost, ease of construction and data collection, and decreased chances for mortality make them attractive tools for monitoring the presence, distribution, and abundance of small mammals. When used in combination with capture–mark–recapture techniques, track tubes may provide researchers with an efficient means of estimating abundances of rare species over large areas (Conroy et al. 2008). Rather than determine abundance with a high degree of accuracy, our goal was to determine whether track tubes could be used to monitor relative abundance through time or between sites. We found that track tubes can be useful for monitoring large fluctuations in the relative abundance of beach mice through time, when abundance estimates are averaged across multiple sites. In addition, track indexes were able to distinguish between sites with the largest differences in abundance (as measured by the M_h jackknife estimator and MKA) within a sample period during periods when mouse abundance and activity were low. This study points to the need to understand factors that influence the relationship between indexes from track tubes and mouse abundance, as well as the importance of designing sampling protocols that produce a strong relationship between these indexes, before track tubes can be used to compare abundance among sites.

ACKNOWLEDGMENTS

We thank reviewers for constructive comments on this manuscript. M. Alley, M. Baker, L. Brown, L. Burch, R. Burdge, S. Claypool, S. Cowen, T. Day, C. Martin, J. McKeithen, B. Miller, B. Miller, M. Occhipinti, M. Striefel, and C. Woodlief provided invaluable assistance in the field. This work would not have been possible without generous access to field sites and logistical support provided by B. Hagedorn, B. Miller, E. Laine, G. Barndollar, and D. Daniels of Eglin Air Force Base. A. Pries, B. Bird, and S. Sneckenberger also provided valuable input during the inception of this study. Funding for this project was provided primarily by the United States Fish and Wildlife Service, with additional assistance from the Florida Fish and Wildlife Conservation Commission.

LITERATURE CITED

BLAIR, W. F. 1951. Population structure, social behavior, and environmental relations in a natural population of the beach mouse (*Peromyscus polionotus leucocephalus*). Contributions from the Laboratory of Vertebrate Biology, University of Michigan 43:1–47.

CONROY, M. J., J. P. RUNGE, R. J. BARKER, M. R. SCHOFIELD, AND C. J. FONNSBECK. 2008. Efficient estimation of abundance for patchily distributed populations via two-phase, adaptive sampling. Ecology 89:3362–3370.

Daly, M., M. I. Wilson, and S. F. Faux. 1978. Seasonally variable effects of conspecific odors upon capture of deer mice (*Peromyscus maniculatus gambelii*). Behavioral Biology 23:254–259.

deRivera, C. E. 2003. Causes of a male-biased operational sex ratio in the fiddler crab *Uca crenulata*. Journal of Ethology 21:137–144.

Drennan, J. E., P. Beier, and N. L. Dodd. 1998. Use of track stations to index abundance of sciurids. Journal of Mammalogy 79:352–359.

Fedriani, J. M., T. K. Fuller, and R. M. Sauvajot. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. Ecography 24:325–331.

Glennon, M. J., W. F. Porter, and C. L. Demers. 2002. An alternative field technique for estimating diversity of small-mammal populations. Journal of Mammalogy 83:734–742.

Gore, J. A., and T. L. Schaefer. 1993. Distribution and conservation of the Santa Rosa beach mouse. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 47:378–385.

Houser, C., C. Hapke, and S. Hamilton. 2008. Controls on coastal dune morphology, shoreline erosion and barrier island response to extreme storms. Geomorphology 100:223–240.

Huber, J. J. 1962. Trap response of confined cottontail populations. Journal of Wildlife Management 26:177–185.

Kaufman, G. A., and D. W. Kaufman. 1994. Changes in body mass related to capture in the prairie deer mouse (*Peromyscus maniculatus*). Journal of Mammalogy 75:681–691.

Legendre, P., and L. Legendre. 1998. Numerical ecology. Elsevier Science, Amsterdam, Netherlands.

Leirs, H., N. Stenseth, J. Nichols, J. Hines, R. Verhagen, and W. Verhagen. 1997. Stochastic seasonality and non-linear density-dependent factors regulate population size in an African rodent. Nature 389:176–180.

Lima, M., N. Stenseth, H. Leirs, and F. Jaksic. 2003. Population dynamics of small mammals in semi-arid regions: a comparative study of demographic variability in two rodent species. Proceedings of the Royal Society, B: Biological Sciences 270:1997–2007.

Loggins, R. E., J. A. Gore, L. L. Brown, L. A. Slaby, and E. H. Leone. 2010. A modified track tube for detecting beach mice. Journal of Wildlife Management 74:1154–1159.

Mabee, T. J. 1998. A weather-resistant tracking tube for small mammals. Wildlife Society Bulletin 26:571–574.

Michener, W. K. 1997. Quantitatively evaluating restoration experiments: research designs, statistical analysis, and data management consideration. Restoration Ecology 5:324–337.

Nams, V. O., and E. A. Gillis. 2003. Changes in tracking tube use by small mammals over time. Journal of Mammalogy 84:1374–1380.

O'Connell, M. A. 1989. Population dynamics of Neotropical small mammals in seasonal habitats. Journal of Mammalogy 70:532–548.

Oli, M. K., N. R. Holler, and M. C. Wooten. 2001. Viability analysis of endangered Gulf Coast beach mice (*Peromyscus polionotus*) populations. Biological Conservation 97:107–118.

Parmenter, C. A., et al. 1998. Small mammal survival and trapability in mark–recapture monitoring programs for hantavirus. Journal of Wildlife Diseases 34:1–12.

Perry, H. R., G. B. Pardue, F. S. Barkalow, Jr., and R. J. Monroe. 1977. Factors affecting trap responses of the gray squirrel. Journal of Wildlife Management 41:135–143.

Prendergast, B. J., L. J. Kriegsfeld, and R. J. Nelson. 2001. Photoperiodic polyphenisms in rodents: neuroendocrine mechanisms, costs, and functions. Quarterly Review of Biology 76:293–325.

Pries, A. J., L. C. Branch, and D. L. Miller. 2009. Impact of hurricanes on habitat occupancy and spatial distribution of beach mice. Journal of Mammalogy 90:841–850.

Pries, A. J., D. L. Miller, and L. C. Branch. 2008. Identification of structural and spatial features that influence storm-related dune erosion along a barrier-island ecosystem in the Gulf of Mexico. Journal of Coastal Research 24:168–175.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org. Accessed 04 October 2008.

Sawada, M. 1999. ROOKCASE: an Excel 97/2000 Visual Basic (VB) add-in for exploring global and local spatial autocorrelation. Bulletin of the Ecological Society of America 80:231–234.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Stanley, T. R., and K. P. Burnham. 1998. Estimator selection for closed-population capture–recapture. Journal of Agricultural, Biological, and Environmental Statistics 3:131–150.

Stanley, T. R., and K. P. Burnham. 1999. A closure test for time-specific capture–recapture data. Environmental and Ecological Statistics 6:197–209.

Stanley, T. R., and J. D. Richards. 2005. Software review: a program for testing capture–recapture data for closure. Wildlife Society Bulletin 33:782–785.

Suazo, A. A., A. T. Delong, A. A. Bard, and D. M. Oddy. 2005. Repeated capture of beach mice (*Peromyscus polionotus phasma* and *P. p. niveiventris*) reduces body mass. Journal of Mammalogy 86:520–523.

Swilling, W. R., M. C. Wooten, N. R. Holler, and W. J. Lynn. 1998. Population dynamics of Alabama beach mice (*Peromyscus polionotus ammobates*) following hurricane Opal. American Midland Naturalist 140:287–298.

Turchin, P., and R. Ostfeld. 1997. Effects of density and season on the population rate of change in the meadow vole. Oikos 78:355–361.

Van Zant, J. L., and M. C. Wooten. 2003. Translocation of Choctawhatchee beach mice (*Peromyscus polionotus allophrys*): hard lessons learned. Biological Conservation 112:405–413.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

Wiewel, A. S., W. R. Clark, and M. A. Sovada. 2007. Assessing small mammal abundance with track-tube indices and mark–recapture population estimates. Journal of Mammalogy 88:250–260.

Submitted 8 July 2011. Accepted 28 October 2011.

Associate Editor was Christine R. Maher.

APPENDIX I

The relationship between track-tube index (cumulative number of tubes with tracks in a grid) and abundance estimated from trapping (M_h jackknife estimator), as a function of the number of days over which the track-tube index was calculated. For each sample period, the asterisk (*) indicates correlations discussed in the text (see ''Materials and Methods'' for further information).