Spatial Patterns in a Population of Nine-banded Armadillos (Dasypus novemcinctus)

W. J. LOUGHRY! AND COLLEEN M. MC DONOUGH

Department of Biology, Valdosta State University, Valdosta, Georgia 31698-0015

ABSTRACT.—Spatial data were collected in a population of individually marked nine-banded armadillos (Dasypus novemcinctus) at a site in Florida from 1992–1995. Approximately 6/ of the animals (118/313) were sighted more than once. Data on distances moved between successive sightings showed that armadillos moved <200 m both within and between years. However, animals moved significantly farther between than within years. The average distance between sightings was significantly longer for adults than for juveniles within, but not between, years. There were no sex differences in distances moved within or between years for either adults or juveniles. Analyses of distances to nearest neighbors showed that adults were closer to one another than to juveniles and that juveniles of the same sex were closer to one another than to juveniles of the opposite sex. This latter result probably reflects maintenance of proximity among littermates.

INTRODUCTION

One of the basic features of any population is the spatial location of its members. Such information can be used to examine population sub-structuring by determining whether particular individuals tend to cluster together (e.g., by kinship, age, sex, etc.). Spatial locations are dynamic, so in addition to knowing where individuals are located at one time, it is necessary to document the extent of their movements (Swingland and Greenwood, 1984). Such data can provide insight into the sizes of individual home ranges/territories and the extent to which individuals are site-loyal.

Nine-banded armadillos (Dasypus novemcinctus) are of interest to behavioral ecologists in part because females give birth to litters of genetically identical quadruplets (Newman and Patterson, 1910; Newman, 1913; Storrs and Williams, 1968; ProdBh et al., 1996). The potential impact of this unusual mode of reproduction on armadillo behavior and social organization has yet to be fully explored (but see Loughry and McDonough, 1994; ProdBh et al., 1996; Loughry et al., 1998). For example, while clonemates are known to be spatially clustered during the 1st summer after emergence from their natal burrows (McDonough and Loughry, 1995; ProdBh et al., 1996), it is unknown whether they remain together as they become older. In addition, the general picture of armadillo spatial patterns is that they have home ranges ranging from 2–20 ha, with considerable overlap between the sexes and, in most populations, between adult females, but with little overlap between reproductively active adult males (Clark, 1951; Fitch et al., 1952; Layne and Glover, 1977; Jacobs, 1979; Galbreath, 1980; Thomas, 1980; Zimmerman, 1982; Breece and Dusi, 1985; Herbst and Redford, 1991; McDonough, 1992; Schell, 1994). While there are anecdotal accounts of fidelity to these ranges over time (Layne and Glover, 1977; Stallknecht et al., 1987), with the exception of McDonough (1992), there are no long-term studies that quantify the number of individuals that remain in a population or the extent to which these individuals move over time. In the present study, we sought to obtain such information in order to gain a better picture of armadillo population structure.

Because of the number of studies of armadillo home ranges (Clark, 1951; Fitch et al.,

1 email: jloughry@valdosta.edu

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in designing the present study it was not clear how much additional insight would be gained by performing yet another such analysis. Thus, instead of gathering large numbers of observations on a relatively small number of animals over a short period of time to generate home range estimates, we used a global positioning system (GPS) to obtain data on large numbers of individuals over a long (4-yr) period. In this study, we recorded the location of each individually marked animal each time it was sighted. These data provide information on spatial relationships which can be used to examine influences on population structure (e.g., clustering of kin might be suggested if members of the same sex were significantly closer to one another than to members of the opposite sex). Many of these animals were sighted more than once in the course of a year and some were resighted between years. Data from these resightings allow us to examine distances moved by individuals over time and provide estimates on the retention and recruitment of individuals into the population.

METHODS

We studied the nine-banded armadillos located on the Tall Timbers Research Station near Tallahassee, Leon County, Florida, during the summers of 1992-1995 (Loughry and McDonough, 1996; McDonough and Loughry, 1997 a). Armadillos were captured using a large dip net attached to a 1–1.5 m pole and then sexed, weighed and measured. Animals were initially aged by weight (McDonough, 1992, 1994; Loughry and McDonough, 1996) as either juveniles (young of the year, <2.5 kg), yearlings (2.5–3.5 kg), or adults (>3.5 kg). Animals were marked for permanent identification using ear tags and, beginning in 1993, passive integrated transponder (PIT) tags. In addition, a small tissue sample for genetic studies was taken from one or both ears using an ear-notcher. These notches were taken from different locations on the ears of different individuals, further contributing to identification of particular animals. Armadillos were marked for long-range identification by supergluing unique colors and shapes of reflective tape on various parts of the carapace. They were then released at the point of capture. The locations of initial sightings and the site of capture (if different) were recorded, but only locations of initial sightings were used in our analyses.

We surveyed the study area for a total of 200 days and 2273 person-h of field time, primarily at night (approximately 16:00–23:00 h), attempting to capture unmarked armadillos and resight previously marked individuals. Censuses were done by car or on foot along roads on the Tall Timbers property (total distance surveyed = ca. 20 km). Whenever a marked armadillo was sighted, we dictated its location and behavior into a tape recorder for later transcription into our field notes. Most of our resightings were separated by ≥24 h, but occasionally we did resight the same individual on the same day. In these cases, sightings were considered independent if they were separated by at least 1 h.

Spatial data were obtained using the Trimble Pathfinder Basic+ Global Positioning System. In August 1994, we used our field notes to locate every sighting of every marked armadillo we had observed during the previous 3 yr (n = 389 sightings of 212 animals). At each location site, we obtained a minimum of 100 readings, which were then corrected and averaged (for a review of GPS procedures, see August 1993) to produce a single x, y coordinate in universal transmercator (UTM) units. We used the same procedures in 1995 except that GPS locations of observed animals were collected every 2–3 wk during the field season (n = 222 sightings of 146 animals). The entire data set for 1992-1995 contained 611 sightings of 313 different individuals.

For analyses of distances moved by armadillos, we used data from all individuals sighted
more than once (n = 118 animals resighted 416 times, mean = 2.88 resightings/individual, range = 2–11). We calculated the distance moved between successive sightings as the hypotenuse of the triangle generated from the x, y coordinates of the last location and the next one. These moves were then classified as to whether they occurred within the same year or between years. Multiple moves by the same individual were averaged within each time category to produce a single value for each animal, except for between-year moves in which the individual also moved into a different age category. We examined these data for sex, age and time (within, vs. between, years) influences with ANOVA, using the Statview statistical package (Abacus Concepts, 1992). To obtain some idea of the extent of armadillo movements, we performed two analyses. First, we calculated the distance moved between the first and last locations of an individual (either within the same year or between years). These data were then analyzed for age and sex differences in distance moved. Second, for each animal, we recorded the longest distance moved between two successive sightings and analyzed these data for age, sex, and temporal differences. Yearlings were excluded from these analyses (and all others) because of small sample sizes (n = 4; see Loughry and McDonough, 1996).

Finally, we examined spatial relationships among armadillos by calculating distances to nearest neighbors. For this analysis, we used data from just 1995. We did this because we caught more animals in 1995 (n = 146; however, three yearlings were excluded from the analysis) than in any other year and so this year presumably provides the most complete picture of the population. Before the analysis, locations of animals that were sighted more than once in 1995 were averaged to produce a single set of coordinates for each individual. Nearest neighbor distances were then calculated by determining the distance of a target animal to every other animal in the population. We then identified the individual juvenile male, juvenile female, adult male and adult female to which the target was closest. The resulting data were analyzed for differences in distances to each age/sex group. It should be noted that these distances were not necessarily reciprocal. For example, adult male A’s nearest juvenile male neighbor might have been X, but juvenile X may actually have had another adult male as his nearest neighbor.

There is one important caveat to our analyses, which is that most of our data are derived from animals sighted on or near roads on the Tall Timbers property. Thus, our data are potentially biased by our largely linear method of sampling. There is no viable sampling alternative given the habitat structure at Tall Timbers (e.g., walking transects would require moving through thick vegetation that would generate so much noise that any armadillos present would flee before we could identify them). However, we feel our data are valuable for the following reasons. First, there are a large number of roads and fire lanes at Tall Timbers that allow us to sample much of the property. Consequently, we do not feel we have missed many opportunities to sight animals. Second, while mark-recapture studies generally miss long-range movements (Koenig et al., 1996), our methods allowed detection of movements by armadillos ranging from 1–1000 m (see below). Thus, it does not appear our data are inherently biased toward movements of a particular magnitude. Third, most of our comparisons are between age and sex classes of armadillos and between different time periods (within vs. between years), so any bias that exists should be the same for all groups and not affect the outcome of these comparisons. Fourth, our analysis of nearest-neighbor distances only deals with individuals that were adjacent to one another, so it would seem least likely to be affected by our sampling methods.

RESULTS

Movement over time.—The mean movement of armadillos at Tall Timbers between successive sightings was generally less than 200 m (range: 0–1180.8 m), both within and be-
Fig. 1.—Average distances (±se) moved by armadillos within and between years at Tall Timbers. Sample sizes are given above each bar.

Analysis of within-year moves showed that adults moved farther on average than did juveniles (F = 12.32, P = 0.0007, df = 1, 83; Fig. 1; range for adults = 2.7–1180.8 m, range for juveniles = 0–205.3 m). However, there were no statistically significant sex differences in distances moved within a year (F = 0.08, P = 0.77), and no significant age or sex differences in distances moved between years (two-way ANOVA, all P > 0.11, df = 1, 66; Fig. 1).

Comparisons of all movements by armadillos showed a significant main effect of time, with animals moving farther between than within years, but no significant effect of age or sex (three way ANOVA, time: F = 23.01, P = 0.0001; age: F = 0.44, P = 0.506; sex: F = 0.73, P = 0.395; in all cases df = 1, 149; Fig. 1). There was, however, a barely significant age × sex interaction (F = 3.99, P = 0.047; Fig. 1).

As a more restrictive test of the effect of time, we compared distances moved between vs. within years for only animals observed in both contexts (n = 43). This analysis also showed that armadillos moved farther between than within years (paired t-test, t = 2.92, P = 0.006, df = 42; means (±se): between years = 163.61 ± 20.90 m, within years = 102.34 ± 6.75 m).

The effect of time may have been due to the increased distances moved by juveniles as they became yearlings. In addition, recruitment of juveniles into our population was very low (i.e., only 12 resightings of juveniles between years, Fig. 1; see also Loughry and McDonough, 1996), so our result may be biased by the extraordinary movements of a few juveniles. However, if one excludes juveniles from the analysis, adults still show the same pattern, moving significantly farther between than within years (t = 3.50, P = 0.0007, df = 113, Fig. 1).

Other measures of armadillo movements were comparable in magnitude to those ob-
TABLE I.—Mean (±se) distance moved between first and last sightings of armadillos at Tall Timbers

<table>
<thead>
<tr>
<th>Age/sex class</th>
<th>n</th>
<th>Distance moved (m)</th>
<th>Range (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult males</td>
<td>43</td>
<td>179.7 (23.19)</td>
<td>2.3–688.1</td>
</tr>
<tr>
<td>Adult females</td>
<td>37</td>
<td>159.6 (15.36)</td>
<td>21.8–1022.9</td>
</tr>
<tr>
<td>Juvenile males</td>
<td>11</td>
<td>127.2 (37.80)</td>
<td>10.7–328.0</td>
</tr>
<tr>
<td>Juvenile females</td>
<td>25</td>
<td>81.3 (20.05)</td>
<td>10.2–527.2</td>
</tr>
</tbody>
</table>

served between successive sightings. For example, the distance moved between the first and last sighting of an individual averaged 147.1 ± 11.8 m (n = 115, pooled over within- and between-year sightings). Comparisons of age and sex differences in these movements revealed a significant effect of age only (F = 6.28, P = 0.014, df = 1,112), with adults moving farther than juveniles (Table 1). In addition, the longest distance moved between two successive sightings averaged 164.4 ± 11.5 m (n = 118; Table 2). A three-way ANOVA of longest distance moved with age, sex and time as the three factors revealed a significant main effect of time (F = 17.23, P = 0.0001, df = 1, 107; Table 2), and a marginally significant age × time interaction (F = 3.67, P = 0.058).

Nearest neighbor distances.—Nearest neighbor distances varied considerably (range = 0–1552.0 m across all age/sex classes). However, in general, adults were significantly closer to other adults than to juveniles (paired t-test, t = 9.88, P < 0.0001, df = 98; Table 3). Surprisingly, juveniles were also significantly closer to adults than to other juveniles (Table 3; paired t = 4.78, P < 0.0001, df = 43; recall that distances are not necessarily reciprocal, see Methods). There were no statistically significant differences in distances of juveniles, adults, males or females to other males or females (Table 3; paired t-tests, all P > 0.09).

Separate examination of nearest neighbor distances for each age/sex group of armadillos revealed significant differences in each case (Table 3). Post-hoc pairwise comparisons showed that adult males were significantly closer to adult neighbors than to juveniles, but were equally close to members of each sex within each age group. The same was true for adult females (Table 3). Juvenile females were equally close to all neighbors except juvenile males, while juvenile males were significantly closer to adult females than to juvenile females (Table 3).

DISCUSSION

The largest previously published field study on the spatial patterns of nine-banded armadillos involved 21 adults and 13 juveniles followed over a total of 13.5 mo (Breece and Dusi, 1985). Thus, the present study broadens our view of armadillo population structure by examining a large number of individuals (n = 313) over a long (4 yr) period of time. Our data indicate that both within- and between-year movements of armadillos are generally

TABLE 2.—Longest distance (mean ± se) moved between successive sightings of armadillos at Tall Timbers within and between years

<table>
<thead>
<tr>
<th>Age/sex class</th>
<th>Within year n</th>
<th>Range (m)</th>
<th>Between years n</th>
<th>Range (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult males</td>
<td>22</td>
<td>10.4–317.9</td>
<td>22</td>
<td>21.8–612.4</td>
</tr>
<tr>
<td>Adult females</td>
<td>19</td>
<td>45.7–1180.9</td>
<td>18</td>
<td>21.8–342.8</td>
</tr>
<tr>
<td>Juvenile males</td>
<td>4</td>
<td>13.5–205.3</td>
<td>5</td>
<td>143.7–318.3</td>
</tr>
<tr>
<td>Juvenile females</td>
<td>22</td>
<td>10.2–156.0</td>
<td>3</td>
<td>159.9–690.1</td>
</tr>
</tbody>
</table>
TABLE 3.—Nearest-neighbor distances (in m, ±SE) between age and sex classes of armadillos at Tall Timbers Research Station in 1995.

F values are from repeated measures ANOVAs within each row, all P < 0.03. Significant (P < 0.05) post-hoc Scheffe tests are indicated as follows: a = adult male vs. adult female, b = adult male vs. juvenile male, c = adult male vs. juvenile female, d = adult female vs. juvenile male, e = adult female vs. juvenile female, f = juvenile male vs. juvenile female.

<200 m, suggesting that at least some members of the population remain in essentially the same area over time. In addition, nearest neighbor analyses indicate that adults are closer to one another than to juveniles and that juveniles of the same sex tend to be closer to one another than to juveniles of the opposite sex.

Sizes of armadillo home ranges vary widely, from ca. 2–20 ha (Clark, 1951; Fitch et al., 1952; Layne and Glover, 1977; Jacobs, 1979; Galbreath, 1980; Thomas, 1980; Zimmerman, 1982; Breece and Dusi, 1985; Herbst and Redford, 1991; McDonough, 1992; Schell, 1994). Assuming that home ranges at our study site are not at the extreme low end of this range (which is a reasonable assumption; Herbst and Redford (1991), working in an area similar to ours, reported home ranges of 3–9 ha for a group of adult females), it appears that armadillos moved less than the diameter of a home range both within- and between-years (see also Layne and Glover, 1977; Stallknecht et al., 1987). While such data might suggest site fidelity, it is important to remember that the majority of the animals in our population were captured only once. Whether these individuals died, engaged in long-distance movements, or remained in the population but were not caught, is unknown. Nine-banded armadillos have been increasing their range throughout the southeastern United States during this century (Humphrey, 1974; Taulman and Robbins, 1996), so clearly some individuals must leave their natal areas. At present, nothing is known about the underlying causes that might generate differences between those individuals that move on and those that remain.

Nearest-neighbor analyses indicated that juvenile armadillos were closer to other juveniles of the same sex, suggesting maintenance of proximity among littermates (see also Prodöhö et al., 1996). This is not surprising because juveniles appear to remain within their natal home range during their 1st summer (pers. observ.). Because juveniles remain in close proximity, the potential for kin-biased behavior appears to exist during this part of the life cycle. Discrimination tests with juveniles show that they can discriminate between siblings and nonsiblings (Loughry and McDonough, 1994), but it is not known whether such discrimination has adaptive consequences in the wild (but see Loughry et al., 1998). The limited movements of juveniles may also explain why so few are collected during the summer as road-kills (Loughry and McDonough, 1996) and would generate the smaller home ranges for juveniles that have been reported (Breece and Dusi, 1985; McDonough, 1992).

Juveniles moved farther between than within years, but between-year moves were still <200 m, so it seems likely that if littermates remain in the population, they could continue to interact. However, there are two lines of evidence that argue against this possibility. First, at least in some populations, juvenile mortality can be quite high (McDonough and Lough-
ry, 1997 b), thus limiting recruitment of juveniles into the population. Limited recruitment was evidenced in the present study by the low number of resightings of juveniles between years. Of 106 juveniles captured between 1992–1995, only 12 (11.3%) had been resighted by the end of 1995 (Fig. 1). Second, DNA fingerprinting analyses of our population have discovered only seven adult sibships (two sets of triplets and five sets of twins from 196 adults examined), with a mean distance between siblings of 455.9 m (Prodohl et al., 1996). These data indicate that most adults are not in close proximity to littermates and that opportunities for kin-biased behavior among adults are quite limited. However, a complete assessment of the potential for interactions between adult kin will require description of juvenile dispersal. To date, no such data have been reported.

While recruitment of juveniles into our population was low, there was some evidence of a sex difference in recruitment with eight of the 12 juveniles recruited being males (Fig. 1). This difference was not statistically significant ($\chi^2 = 1.33, P > 0.20$); however, there are two other lines of evidence that suggest males may be more likely to remain in their natal population. First, in 1997 we documented six additional cases of juvenile recruitment, all of which involved males, making the sex difference in recruitment significant ($\chi^2 = 5.56, P < 0.025$). Second, all of the seven adult sibships identified in our population by DNA fingerprinting were male. At present, we have no data that would explain why this sex difference in recruitment occurs.

Adult armadillos also moved relatively short distances. As argued above, these limited movements may not generate any benefits from associating with kin, but other advantages are possible. For example, adults could benefit by developing long-term relationships with individuals whose home ranges overlap their own. Such relationships between the sexes could be advantageous in acquiring mates and, within sexes, by reducing the costs of resource defense and aggression (McDonough, 1994). Adults moved farther between than within years, suggesting some fluidity to an individual’s home range over time. These movements may reflect changes in resource distributions or social context (e.g., vacancies opening up due to the death or dispersal of a neighbor).

Adults were significantly closer to adult neighbors than to juveniles. Juveniles are often targets of adult aggression (McDonough, 1994), so it may be that juveniles are avoiding adults. However, this seems less likely because examination of juvenile nearest neighbor distances showed that juveniles were significantly closer to adults than to other juveniles. It seems more probable that these results stem from the reproductive biology of armadillos. As stated above, juveniles tend to remain close to their natal burrow during much of their 1st summer and, consequently, within their mother’s home range (McDonough, 1992). Thus, every juvenile is likely to have at least one adult close by (Prodöhl et al., 1998). The same is not true for adults. Many adults apparently do not reproduce in a given year (Prodöhl et al., 1998), so they do not have any juveniles nearby. Presumably, adults have other adults as their nearest neighbors because of the effect of these nonreproductive individuals on the calculation of distances to juveniles.

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