Patterns of Mortality in a Population of Nine-banded Armadillos, Dasypus novemcinctus

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ABSTRACT.—We used data from carcasses found in a natural population of nine-banded armadillos (Dasypus novemcinctus) to assess the sources and age structure of mortality. Juveniles (young of the year) made up approximately 33% of the living population, but constituted about 60% of all carapaces collected. Circumstantial evidence indicated that most juvenile, but not adult, mortality was probably due to predation. Increased adult mortality was associated with a period of prolonged drought.

INTRODUCTION

Describing patterns of mortality is crucial for understanding the population biology and life-history patterns of a species (Caughley, 1977; Derocher and Stirling, 1996). However, obtaining such information for wild populations of animals is difficult. Ideally, one would observe a cohort of individuals throughout their lifetime and record the number of individuals that die at each particular age. This technique is difficult and time-consuming, requiring extensive and exhaustive monitoring of the population. Alternatively, one could obtain cross-sectional data by noting the number of individuals in different age classes that die within a particular period. This method is also problematic because deaths are rarely observed and, in many cases, can not be distinguished from long-distance dispersal.

Another issue concerning mortality patterns is their consistency over time. Assuming patterns of mortality can be determined, these patterns may change due to environmental events such as drought (Ralls and White, 1995), flooding, fire, and/or changes in predator abundances.

The nine-banded armadillo (Dasypus novemcinctus) is a case where inferring mortality is difficult because this species is solitary (Clark, 1951) and typically occurs in thickly vegetated habitats (Clark, 1951; Talmage and Buchanan, 1954). However, armadillos possess a tough protective carapace that decomposes slowly in moderately xeric environments (McDonough, pers. observ.) and usually is not ingested by predators or scavengers. These carapaces can provide information about the age of the deceased animal and possible cause of death (e.g., puncture wounds might indicate predation). In this study we collected carapaces from a population of armadillos in S Texas and used them to identify patterns and possible causes of mortality. In addition, data were collected for 4 yrs during which a drought occurred, so we were able to look at changes in patterns of mortality that were associated with changes in environmental conditions.

METHODS

This study was conducted on the Rob and Bessie Welder Wildlife Refuge, San Patricio Co., Texas (for full description see Drawe et al., 1978; McDonough, 1992). Data were collected over 4 yrs (1988–1991; 31 months, January–March 1988, July 1988 through October 1989, March through October 1990, January 1991; May through July 1991) for a total of 1577 h of field time. During this time a drought occurred (most severe during July 1989–October 1989), with rainfall only 20.5% of a 32-yr average (Welder weather records; L. D. Drawe, pers. comm.).
Carapaces of dead armadillos were collected during regular surveys of the refuge. Because we were interested in naturally occurring mortality, road-killed animals were not included in the sample. Areas were routinely sampled so that carapaces were not on the ground for long periods of time (e.g., typically less than 1 mo). Carapaces were usually easy to collect because they were conspicuous in the short vegetation of the refuge and because they tended to bleach over time.

In order to evaluate the age structure of armadillo mortality, we needed to assign the collected carapaces to a particular age group. Live-caught armadillos at Welder were assigned to age categories based on body weight (McDonough, 1994). Juveniles (i.e., young of the year) were individuals weighing ≤2.5 kg if caught between April and September. If an animal was first caught between October and February, it was classified as a juvenile if its weight was ≤3 kg (McDonough, 1994). Individuals weighing more than 3.5 kg at initial capture were classified as adults. Only one individual (out of 194) weighed between 3.0 kg and 3.5 kg at initial capture and was classified as an adult to be conservative. In addition to weights, we obtained five measures of body size (all in centimeters): (1) tail base = the circumference of the tail at its juncture with the body near the pelvic shield of the carapace; (2) tail length = the length of the tail from the base to the tip (animals who were missing a portion of the tail were not measured); (3) front carapace = the length of the anterior edge of the scapular shield of the carapace (i.e., at the juncture with the head), measured from the bottom of the right side of the animal to the bottom of the left side; (4) front band = the length of the posterior edge of the scapular shield (measured from the bottom right to bottom left side of the animal), and (5) back band = the length of the anterior edge of the pelvic shield, i.e., the ninth, most posterior, movable band (measured from the bottom right to bottom left side of the animal). These measurements correlate significantly with weight, with length of the front band exhibiting the strongest relationship in a multiple regression (Loughry and McDonough, 1996). Thus, because we could not use body weight to assign carapaces to a particular age category, we used length of the front band. Carapaces were classified as juveniles if the front band was ≤29 cm; all others were classified as adults. Some carapaces were incomplete or deteriorated and we used whatever measurements were available to assign them to an age group. This seems justifiable because all body size measurements correlate significantly with weight and differ significantly between juveniles and adults (see Loughry and McDonough, 1996).

To assess the relative risk of mortality for each age class, we compared the proportion of carapaces in a particular age group with the proportion of live-caught individuals of that age group. To determine the effect of the drought on patterns of mortality, the numbers of adult and juvenile carapaces collected during the drought period were compared to those collected before and after the drought. We divided each year into four quarters beginning with January 1988. The first four quarters when we were at Welder were considered the pre-drought period (quarters 1, 3 and 4 of 1988, and quarter 1 of 1989; quarter 2 of 1988 was not included because we were not at the refuge). The next five quarters were considered the drought period (quarters 2, 3, 4 of 1989 and 1 and 2 of 1990). The two quarters (3 and 4 of 1989) when the drought was most severe were included here as well as the quarter before and two quarters after. We included these two latter quarters because carapaces found then seemed old and probably were the result of the drought. The post-drought period included carapaces collected during the remaining four quarters (3 and 4 of 1990 and 1 and 2 of 1991). The number of carapaces collected in each quarter was compared to expected values calculated from the proportion of time spent observing in each period. For example, since 39.9% of total observation time occurred during the pre-drought period, one would expect 39.9% of the carapaces to be collected during that time.
TABLE 1.—Numbers of live and dead armadillos found on the Welder Wildlife Refuge, 1988–1991

<table>
<thead>
<tr>
<th>Age class</th>
<th>Dead</th>
<th>Expected*</th>
<th>Live</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juveniles</td>
<td>43</td>
<td>23.6</td>
<td>111</td>
</tr>
<tr>
<td>Adults</td>
<td>29</td>
<td>48.4</td>
<td>227</td>
</tr>
</tbody>
</table>

*Expected numbers of dead individuals are based on the proportion of live individuals

Sources of mortality were evaluated by inspecting the carapaces for tooth or claw marks that might indicate predation. Marks were designated as bite marks if they were small (5 mm–10 mm) and the force was directed inwardly. While we cannot be sure that such marks were responsible for the animal’s death (instead of the result of subsequent scavenging), they at least provide a preliminary assessment of the importance of predation in armadillo mortality.

Comparisons between ages of dead and live individuals and between patterns of mortality during drought and non-drought periods were made using chi-square goodness-of-fit tests. The binomial test was used to analyze post-hoc two-way comparisons. Fisher’s exact test was used to determine differences in the incidence of puncture marks in juveniles and adults. Significance levels were set at $P \leq 0.05$.

RESULTS

A total of 72 carapaces was collected and measured (Table 1). Juveniles were significantly over-represented and adults under-represented among dead individuals (chi-squared goodness of fit test, $X^2 = 23.73$, df = 1, $P < 0.0001$).

Of the 72 carapaces collected, 29 were examined for evidence of predation (the remaining carapaces were measured, but details about their condition were not recorded). Of these 29, 15 of 21 juvenile carapaces exhibited bite marks, but 0 of 8 adult carapaces had bite marks. This age difference in the possible incidence of predation was significant (Fisher’s exact test, $P = 0.0007$).

Examination of carapaces collected quarterly during the study showed that juvenile mortality patterns differed from those of adults (Fig. 1). Each year (1988–1990), juvenile mortality peaked during the third quarter (July–September) and was relatively low and constant the rest of the year (Fig. 1). Adult mortality was relatively low during 1988, then increased during 1989 and decreased again after the second quarter of 1990. In order to examine the effects of drought on patterns of mortality, the number of juvenile and adult carapaces collected prior to, during and after the drought were compared to expected values (Table 2). When juvenile and adult carapaces were pooled, the distribution between the three periods did not differ significantly from expected ($X^2 = 3.51$, df = 2, ns; Table 2). However, when each period was considered separately in a post-hoc two-way comparison, more carapaces were found during the drought than expected (Table 2). When juveniles and adults were considered separately, more adult carapaces were collected during the drought than expected and less before the drought ($X^2 = 14.07$, df = 2, $P < 0.001$), whereas juvenile mortality patterns did not differ significantly from expected ($X^2 = 0.679$, df = 2, ns).

DISCUSSION

Unlike many solitary animals which leave few clues regarding how and when they died, nine-banded armadillo carapaces provide a valuable database for describing mortality patterns in this little-known species. Overall, juveniles had a higher risk of mortality than adults in this population. This is a relatively common pattern for mammals (reviewed in Caughley,
Fig. 1.—Temporal distribution of juvenile and adult carapaces collected at the Welder Wildlife Refuge, 1988–1991. Years are divided into quarters, beginning with January 1988. No sampling occurred during quarter 2 of 1988.

1966) and could be due, among other things, to higher rates of malnutrition in young (Guinness et al., 1978; Packer et al., 1988; Derocher and Stirling, 1996) and/or higher rates of predation (Cheney and Wrangham, 1986; Longland and Jenkins, 1987; Temple, 1987; Ralls and White, 1995; Smith and Anderson, 1996). The higher frequency of puncture

<table>
<thead>
<tr>
<th>Time period</th>
<th>Proportion of observation time</th>
<th>Total</th>
<th>Adult</th>
<th>Juvenile</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predrought</td>
<td>0.399</td>
<td>21 (27.5)</td>
<td>4 (11.2)**</td>
<td>17 (16.4)</td>
</tr>
<tr>
<td>Drought</td>
<td>0.374</td>
<td>33 (25.9)**</td>
<td>20 (10.5)**</td>
<td>13 (15.3)</td>
</tr>
<tr>
<td>Postdrought</td>
<td>0.226</td>
<td>15 (15.6)</td>
<td>4 (6.3)</td>
<td>11 (9.3)</td>
</tr>
</tbody>
</table>

* Expected values in parentheses
** Binomial test; P < 0.05
*** Binomial test; P < 0.01
wounds in juvenile as compared to adult carapaces suggests that increased juvenile mortality is largely due to predation. In fact, if predators often dismember or consume juvenile carapaces, thus preventing collection of the remains, our data may underestimate the importance of predators as a source of juvenile mortality. Because juvenile armadillos are smaller and their carapaces are more pliable, they should be vulnerable to more predators than adults. This greater vulnerability may be manifested in various aspects of juvenile behavior. For example, juveniles have greater flight distances from humans and are active much earlier in the day than are adults (McDonough and Loughry, 1995, 1997).

While predation seems to be an important source of armadillo mortality at our study site, it is unclear what is preying on them. Known predators of armadillos in the United States include puma, *Felis concolor* (Carr, 1982; Maehr *et al.*, 1990), American black bear, *Ursus americanus* (Harlow, 1961; Maehr and Brady, 1982) and the American alligator, *Alligator mississippiensis* (McNease and Joenan, 1977; Shoop and Ruckdeschel, 1990). However, except for alligators, these species are either rare or absent on the refuge, and alligators presumably would not leave carapace remains on land. Additional possibilities (at least for juveniles) include raptors (a red-tailed hawk, *Buteo jamaicensis*, nest contained a juvenile carapace; C. Sisson, pers. comm.), coyotes, *Canis latrans* and bobcats, *Lynx rufus* (Carr, 1982). For the latter two species, stomach content and fecal analyses have not confirmed predation on armadillos (Beasom and Moore, 1977; Fritts and Sealander, 1978; Maehr and Brady, 1982; Andelt *et al.*, 1987; Windberg and Mitchell, 1990); however, few of these studies have been conducted at the time of year (*i.e.*, early summer) when juveniles are presumably most vulnerable (but see Andelt *et al.*, 1987; Maehr and Brady, 1986).

Adult mortality was rarer than juvenile mortality. Adults have been reported killed by many of the species mentioned above (Harlow, 1961; McNease and Joenan, 1977; Carr, 1982; Maehr and Brady, 1982; Shoop and Brady, 1982; Maehr *et al.*, 1990; Shoop and Ruckdeschel, 1990), but it seems likely that they are taken less often as prey than are juveniles, presumably because adults are larger and have more experience at avoiding predators. Indeed, in the present study we found no evidence of predation on any of the adult carapaces we examined. Although one could argue that predation occurs on adults without leaving evidence on the carapace (*e.g.*, if a predator rolled an adult onto its back and attacked the soft underparts), it seems more likely that other sources of mortality may be more important. For example, diseases such as leprosy may kill many adults (Meyers *et al.*, 1978; Truman *et al.*, 1986). In our study site, 17% of individuals have antibodies to a specific antigen of *Mycobacterium leprae*, indicative of exposure to leprosy, and about 30% of the adults harbor the bacterium (Truman *et al.*, 1991). Mortality due to leprosy solely affects adults since no juveniles were found to be infected (Truman *et al.*, 1991).

Late summer appears to be a critical period for juvenile mortality, perhaps because juveniles are becoming more independent, *e.g.*, foraging alone without their siblings (McDonough, pers. observ.), and consequently more at risk from predators. Not surprisingly, the increase in collection of juvenile carapaces in late summer corresponds to a decrease in live juveniles observed on the refuge (McDonough, 1994). The high juvenile mortality found in this study may also explain the low recruitment of young into some armadillo populations (Loughry and McDonough, 1996; McDonough, 1992).

Mortality during the drought was severe. In an area closely monitored during this period, 88% of the armadillos died or emigrated during the 4 most severe mo of the drought and 0% of the original population remained 3 mo after the drought ended (McDonough, 1992). Drought influenced the patterns of mortality in this population, but only for adults. This is surprising because drought should impact all age classes equally. One possible explanation is that there may have been less reproduction during this period. Female armadillos give
birth to identical quadruplets once a year in March (Enders, 1966). They breed during the summer and routinely delay implantation until November (Enders, 1966). Armadillos have been known to delay implantation during stressful periods, such as captivity, for up to 2 yr (Storrs et al., 1988). Presumably, this physiological response functions in the wild to allow females to adjust their reproductive efforts to prevailing environmental conditions (Sandell, 1990). If fewer females reproduced in 1989 because of drought, there would be fewer carapaces of juveniles to be collected subsequently.

Finally, it is important to note that the mortality patterns described here are due to natural sources. These patterns are dramatically different from those derived from other sources. For example, road-killed armadillos were almost exclusively adults (Loughry and McDonough, 1996). Adults range further, so presumably they encounter automobiles more frequently, and thus end up as road-kills more often (Loughry and McDonough, 1996). However, for the various reasons discussed earlier, juveniles would be expected to have higher mortality from natural causes. Nonetheless, these differences in mortality patterns again highlight the limits in using data on road-killed animals to infer armadillo population features (c.f., Loughry and McDonough, 1996).

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Literature Cited


