Impacts of land management practices on a population of nine-banded armadillos in northern Florida

Colleen M. McDonough and W. J. Loughry

Abstract Over a 12-year period (1992–2003), we examined the impact of prescribed burning and hardwood removal on a population of nine-banded armadillos (Dasypus novemcinctus) located at Tall Timbers Research Station just north of Tallahassee, Florida. Although these armadillos are often found in close proximity to humans, there currently are no data on how they are affected by human impacts on the environment. Responses to annual burns between 1992–1997 indicated that in some years armadillos, particularly adults, avoided areas that had been burned, but effects were inconsistent and relatively weak. In contrast, hardwood removal during 1998–2000 coincided with a significant decline in population numbers that continued through 2003. However, interpretation of hardwood removal effects was complicated by the occurrence of a severe drought during the same time period. Comparisons between animals in logged and unlogged parts of the study area during the period of hardwood removal revealed few differences, suggesting drought was an important influence. However, because our population continued to decline after the drought ended, it seems likely that hardwood removal generated more persistent effects that were temporarily masked by the drought. We observed armadillos frequently in logged areas, probably because few other habitat choices were available. Armadillos weighed less during and after hardwood removal than prior to it. Although adult reproductive behavior appeared largely unaffected by logging, numbers of juveniles captured and recruited declined significantly with the onset of hardwood removal. There was no evidence that the disturbance from logging caused increases in distances moved by animals that remained in the study area. Our results may have broader implications for predicting how armadillo populations in Latin America will be affected by similar land management practices.

Key words armadillo, Dasypus novemcinctus, fire, Florida, hardwood removal

A fundamental issue in conservation biology is understanding how humans affect animal populations (Soucé and Wilcox 1980). Both positive and negative effects may occur in a number of ways, including fairly obvious, direct impacts such as hunting (e.g., Hill et al. 1997, Fitzgibbon 1998) and far more subtle and indirect effects such as habitat fragmentation, pollution, and global warming (Meffe and Carroll 1997). Humans inevitably alter their environment, whether intentionally or not, with potentially important consequences for the associated wildlife of the area. A conspicuous example of this is the use of fire to alter vegetation structure within an area. While fire has undeniable
benefits for maintaining certain ecosystems (e.g., open, pine [Pinus sp.]-dominated forests, Stoddard 1962), clearly some resident animal species may be impacted negatively by its occurrence. Similarly, humans often modify vegetation (e.g., by logging) to the benefit of some species and the detriment of others.

The nine-banded armadillo (Dasypus novemcinctus) is a medium-sized (adult body weight: 3-6 kg) mammal found throughout much of the southeastern United States (Taulman and Robbins 1996). This species exhibits obligate polyembryony (Loughry et al. 1998, Enders 2002), whereby females, after mating during the summer, implant a single fertilized egg in the late fall that divides into 4 embryos, so that females give birth to a single litter of genetically identical quadruplets the following spring. Aside from adult males and females associating during the mating season (May-August, McDonough 1997) and juvenile littermates maintaining proximity to one another during their first weeks above ground, nine-banded armadillos are relatively asocial (McBee and Baker 1982). Armadillos dig burrows in which they sleep 18-20 hours a day (McNab 1980). When active above ground, they spend much of their time alone, foraging in the soil and leaf litter for various invertebrates (McBee and Baker 1982, Redford 1985). While armadillos may be observed in a variety of environments, in the United States they seem to prefer bottomland hardwood forests (Inbar and Mayer 1999, McDonough et al. 2000). Most burrows are found in this type of habitat, and it seems animals concentrate their activity there, occasionally moving out into other areas. Although armadillos often are found in close proximity to humans, there are no studies describing armadillo responses to human impacts on the environment.

As part of a long-term study of armadillo behavior and ecology, we monitored a population of nine-banded armadillos at the Tall Timbers Research Station, located just north of Tallahassee, Florida, each summer between 1992 and 2003. As part of its land management plan, Tall Timbers engages in a yearly program of prescribed burning that includes many areas used by armadillos. In 1998 Tall Timbers decided to eliminate hardwoods from much of the property in an attempt to restore open, upland pine habitat for the northern bobwhite (Colinus virginianus). This entailed a 3-year (1998-2000) program of hardwood removal, with some subsequent planting of logged areas with pine seedlings. Annual burns and hardwood removal both represent dramatic and potentially significant impacts on resident animal populations. In this paper we examine how nine-banded armadillos responded to these practices. We predicted that armadillos would respond negatively to hardwood removal because this represented a significant loss of preferred habitat. Burning also represents a loss of habitat, albeit less permanently, so we predicted that armadillos would respond negatively to burning as well.

**Study area**

Tall Timbers, 1,600 ha in size, was situated along the north shore of Lake lamonia (Figure 1a). Brennan et al. (1998; see also McDonough et al. 2000) identified 3 main habitat types at Tall Timbers: 1) hammocks, which were bottomland hardwood forests consisting primarily of oak (Quercus spp.), American beech (Fagus grandifolia), and southern magnolia (Magnolia grandiflora); 2) fields, which were plowed annually and planted with corn (Zea mays), clover (Trifolium spp.), and brown top millet (Urochloa ramosa); and 3) upland pine areas, consisting of loblolly (Pinus taeda), shortleaf (P. echinata), and some longleaf (P. palustris) pines. Hammocks were characterized by a closed canopy of hardwoods with little understory. Fields were open areas with thick ground cover, and upland pine consisted of open woodlands with considerable ground cover in the form of grasses and shrubs. Previous work indicated that most armadillo burrows and sightings of active animals were in hammocks (McDonough et al. 2000). While some animals may have had home ranges centered within the 2 other habitat types, it appeared most armadillo activity in field and upland pine areas was the result of animals moving from hammocks in search of food (McDonough et al. 2000).

Because armadillos appeared to predominantly use hammocks, our study area did not include the entire Tall Timbers property but instead centered on that subsection along the lakefront where hammocks were located (Figure 1a). To obtain an estimate of total study area, we took all the positions of all animals in all years (i.e., all of the points in Figure 1a) and used ArcView (Environmental Systems Research Institute 1999) to create a 250-m buffer around each point. We then merged these areas into a single, unified space. The 250-m buffer was a
reasonable estimate as it was very close to the average distance armadillos moved between successive sightings (Loughry and McDonough 1998, 2001) and thus was likely to encompass most of the habitat used by a particular individual. Using this technique, our study area across all years encompassed 1,171 ha.

Methods

Data were collected at Tall Timbers each summer (May–August) from 1992 through 2003 (for details, see McDonough and Loughry 1997a, Loughry and McDonough 1998). There were only 2 days of sampling in 1996 and 8 days in 2000; in other years num-

Figure 1. (a) Map of Tall Timbers Research Station, Florida, showing major habitat types. Open circles indicate locations of all armadillos sighted 1992–2003 ($n = 2,047$). Although classified as upland pine, many hardwoods were found in this habitat type prior to 1998; (b) Areas at Tall Timbers subjected to prescribed burning 1992–1997. Note that the entire area was not burned each year (see Table 1); (c) Areas logged at Tall Timbers during 1998–2000.
ber of sampling days varied between 45–63 (Robertson et al. 2000). We conducted censuses for armadillos from ca. 16:00 to 24:00 hours each day by walking or driving along roads and paths on Tall Timbers. We used spotlights to observe animals after dark. We captured armadillos using long dip nets. Captured animals were weighed, sexed, measured, marked for visual identification with various shapes and colors of reflective tape glued to the carapace, and marked for permanent identification with 1 or 2 fingerling fish tags attached to the ears and, beginning in 1993, with passive induced transponder (PIT) tags injected under the skin on the dorsal side of the neck. We assigned animals to 3 age categories (juvenile, yearling, adult) on the basis of weight (Loughry and McDonough 1996). However, because differences between adults and yearlings were minimal, in all the analyses reported here we pooled data from yearlings and adults, and hereafter we refer to all animals >1 year old as adults. We obtained spatial locations of animals when captured and resighted using a handheld Global Positioning System (GPS, see Loughry and McDonough 1998).

We used data from captured animals for all GIS analyses and all other analyses where we needed to know the precise identity of an individual. With one exception, we averaged multiple measures for an individual where appropriate (e.g., for weights and distances moved) to avoid pseudoreplication. The one exception involved the GIS analyses, where we used all sightings of all animals. We did this because individuals could move among habitat types and using all locations provided the most complete picture of space use. Averaging multiple locations into a single value would obscure and possibly even misrepresent spatial patterns in our population. Although we did use multiple locations from the same animal in these analyses, problems with pseudoreplication and autocorrelation were likely to be low because the average number of resights for an individual within a year typically was <3, with an average >7 days between successive sightings (Loughry and McDonough 2001). Because we often saw animals that we were unable to catch, we used data on overall number of sightings of animals per hour of observation to determine population abundance (as in McDonough and Loughry 1997a, Robertson et al. 2000). In this instance, while we did not know the precise identity of an individual, we could usually assign animals to age categories (juvenile or adult) on the basis of body size.

**Effects of burning**

Prescribed burning at Tall Timbers primarily targeted upland pine areas (Figure 1b). However, the amount of area burned varied among years because of variation in suitable weather conditions and other factors. Consequently, we analyzed data on effects of burning for each year independently. To avoid confounding effects of burning with those of hardwood removal, we only examined fire effects prior to onset of logging (i.e., 1992–1997).

For armadillos, fire presumably represents a temporary loss of vegetative cover and possibly reduced foraging success due to fewer invertebrates available in the upper layers of burned soils. Consequently, we predicted that armadillos would avoid burned areas, especially those burned recently. To test this assumption we used ArcView to obtain the percentage of our study area burned each year. We further subdivided burn data by when the burn occurred: winter burns were those areas burned between December–February and spring-summer burns occurred between March–August. As our census typically began in late May or early June each year, we reasoned that armadillos might not avoid areas burned during winter because these areas would have had sufficient time to regenerate but would avoid more recently burned areas (i.e., those burned just prior to or during our field season). With these data we then used chi-square tests to compare expected and observed frequencies of observations of armadillos in burned and unburned areas. Because of the potential for age differences in response, we performed these analyses separately for adults and juveniles.

**Effects of hardwood removal**

Over the period 1998–2000, logging at Tall Timbers removed hardwoods not located adjacent to the lakefront (Figure 1c) and affected about 51% (597.4 ha) of our study area. In total, 32,371.19 tons of hardwood pulpwood were removed (E. Staller, Tall Timbers Research Station, personal communication). We analyzed effects of hardwood removal on our armadillo population in the following ways: 1) we examined changes in population abundance by comparing numbers of animals observed per hour of observation across the 3 time periods of before (1992–1997), during (1998–2000), and after (2001–2003) hardwood removal; 2) we examined effects of hardwood removal on reproduction by comparing proportions of females classified as lactating, not lactating, or possibly lactating (as defined
in Loughry and McDonough 1996) across the same 3 time periods. We also compared frequency of sightings of mating pairs (McDonough 1997), proportion of the population comprised of juveniles, and number of litters captured before, during, and after hardwood removal; 3) we reasoned that a large-scale disturbance such as hardwood removal might induce some animals to leave the study area completely, causing rates of juvenile recruitment and adult retention within the population to decline. For juvenile recruitment we tested this prediction by comparing proportions of juveniles born in each of the 3 time periods that were subsequently recaptured in a later year. For adult retention we compared proportions of adults caught in more than 1 year within each of the 3 time periods. Declines in recruitment or retention might be further reflected in distances animals moved as they tried to avoid disturbed areas and find suitable habitat. We analyzed this by comparing distances moved between successive sightings of an animal, both within a year for each of the 3 time periods and between years (between-year moves were classified by time period based on the year the move was completed; i.e., the between-years movement of an animal last seen in 1995 and then again in 1998 was assigned to the “During” hardwood removal time period). Because lengths of adult and juvenile movements differ significantly (Loughry and McDonough 1998, 2001), we analyzed all movement data separately for each age group; and 4) we analyzed changes in space use by using ArcView to determine proportions of all armadillo sightings that occurred within logged areas before, during, and after hardwood removal. We used chi-square tests to compare these proportions, again doing so separately for adults and juveniles.

**Drought**

Analyses of hardwood removal effects were complicated by the fact that a severe drought occurred in north Florida coincident with the period of hardwood removal. Cumulative rainfall totals for 1998–2000 were 111 cm below the 30-year average for the region (United States National Climatic Data Center 2005). Hardwood removal and drought were both unique, one-time events, so the absence of replicates and planned controls makes disentangling the effects of each difficult. Nonetheless, we attempted to do so by comparing armadillos captured in areas that were logged with those in areas that were not. Unlogged areas of the study site consisted of 2 sets of islands as well as 2 large mainland hammocks (i.e., the white areas along the lakefront in Figure 1c). We performed 2 sets of analyses. First, we compared armadillos in logged and unlogged areas during the period of hardwood removal, reasoning that if logging was the primary influence, then animals in unlogged areas would not be affected and thus would exhibit differences from those in logged sites (alternatively, a lack of differences between the 2 areas would suggest that drought was the primary influence). Second, we compared animals in unlogged areas before the drought (1992–1997) versus during the drought, predicting that if drought was important, we should see differences in the animals between the 2 time periods (and, alternatively, a lack of differences between the 2 time periods would indicate that drought was not a major impact). For the same reasons outlined above, we performed all analyses separately for juveniles and adults.

**Results**

**Burning**

Effects of fire on space use by armadillos at Tall Timbers revealed few consistent patterns (Table 1).

Table 1. Observed (and expected) frequencies of observations of juvenile and adult armadillos in burned and unburned areas at Tall Timbers, Florida between 1992–1997.

<table>
<thead>
<tr>
<th>Year</th>
<th>Winter</th>
<th>Spring-summer</th>
<th>Unburned</th>
<th>( \chi^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>13.6</td>
<td>4.4</td>
<td>82.0</td>
<td>6.97 *</td>
</tr>
<tr>
<td>Adults</td>
<td>4 (10.9)</td>
<td>0 (3.5)</td>
<td>76 (65.6)</td>
<td></td>
</tr>
<tr>
<td>Juveniles</td>
<td>0 (7.1)</td>
<td>0 (2.3)</td>
<td>52 (42.6)</td>
<td>9.85 **</td>
</tr>
<tr>
<td>1993</td>
<td>13.60</td>
<td>27.7</td>
<td>58.7</td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>7 (18.1)</td>
<td>26 (36.8)</td>
<td>100 (78.1)</td>
<td>9.48 **</td>
</tr>
<tr>
<td>Juveniles</td>
<td>0 (6.8)</td>
<td>19 (13.9)</td>
<td>31 (29.3)</td>
<td>7.82 *</td>
</tr>
<tr>
<td>1994</td>
<td>0.40</td>
<td>25.4</td>
<td>74.2</td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>0 (0.3)</td>
<td>1 (17.0)</td>
<td>66 (49.7)</td>
<td>16.43 ***</td>
</tr>
<tr>
<td>Juveniles</td>
<td>0 (0.04)</td>
<td>0 (2.5)</td>
<td>19 (7.4)</td>
<td>3.53</td>
</tr>
<tr>
<td>1995</td>
<td>1.8</td>
<td>26.0</td>
<td>72.2</td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>8 (2.8)</td>
<td>22 (40.8)</td>
<td>127 (113.4)</td>
<td>8.82 *</td>
</tr>
<tr>
<td>Juveniles</td>
<td>4 (1.1)</td>
<td>14 (15.6)</td>
<td>42 (43.3)</td>
<td>1.95</td>
</tr>
<tr>
<td>1997</td>
<td>5.7</td>
<td>19.8</td>
<td>74.5</td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>7 (8.2)</td>
<td>23 (28.3)</td>
<td>113 (106.5)</td>
<td>0.72</td>
</tr>
<tr>
<td>Juveniles</td>
<td>0 (1.2)</td>
<td>5 (4.2)</td>
<td>16 (15.6)</td>
<td>1.11</td>
</tr>
</tbody>
</table>

- Areas burned between December–February.
- Areas burned between March–August.
- Total size of the study area was 1,171 ha.
- \* \( P < 0.05 \), \** \( P < 0.01 \), \*** \( P < 0.001 \)
In some years armadillos seemed to avoid burned areas (e.g., 1992-1994), but in others sightings were randomly distributed (e.g., 1997, Table 1). Consistent with expectation, in 4 of 5 years (1992-1995), adults appeared to avoid more recently burned areas, but juveniles did not (Table 1).

**Hardwood removal**

Numbers of armadillos (adults and juveniles combined) observed per hour of field time varied considerably between years (Figure 2). Abundance changed significantly over the 3 time periods, being highest while logging was ongoing but declining to the lowest levels after hardwood removal was complete (Table 2). The peak in abundance during logging was due to adults; juvenile abundance was highest prior to logging and was low both during and after completion of hardwood removal (Table 2).

Low juvenile abundance after the onset of logging did not appear to be entirely the result of changes in adult reproductive behavior (Table 3). For example, observations of reproductive pairs were actually highest during logging but similar during pre- and post-logging periods. However, distributions of female lactational status indicated that a greater proportion of females were found not lactating during the period of hardwood removal (Table 3). Thus, while adults continued to mate during the logging period, many of these reproductive attempts apparently failed. This was further supported by the facts that a) the number of litters found per day in the field was highest prior to logging and declined thereafter (Table 3); b) the proportion of the population comprised of juveniles also was highest prior to logging and remained low through the post-logging period (Table 3); and c) juvenile recruitment was significantly lower during and after hardwood removal than before (Table 2).

We found no support for the hypothesis that disturbance promoted increased movement, either by adults or juveniles, or within or between years (Table 2). However, body weights did change: adults and juveniles were significantly heavier prior to logging than during or after (Table 2). Proportions of sightings of juveniles in logged areas did not change during the study, but adult sightings actually increased after the completion of logging (Table 2). Although juvenile recruitment declined with the onset of logging, the proportion of adults retained in the population was higher during logging than before or after (Table 2).

**Drought**

We found few differences between juvenile or adult armadillos from logged versus unlogged areas of the study site during the period of hardwood removal and drought (Table 4), consistent with the hypothesis that all animals were similarly impacted by drought, with little differential response due to hardwood removal (t-test comparisons for weights and distances moved, chi-square for proportions). However, juveniles in unlogged areas weighed less than their counterparts in logged areas ($t=3.99, P=0.0003$), adults from logged areas moved farther between years than did adults from unlogged areas ($t=1.98, P=0.05$), and nearly twice as many adults were captured in logged than in unlogged areas ($\chi^2 = 57.67, P<0.0001$, Table 4). Comparisons of juveniles and adults from unlogged areas before versus

**Figure 2.** Average abundance (± SD) of armadillos at Tall Timbers, Florida during each year of the study. Number of sampling days and number of hours of observation per year are provided above each point. Number of observers was 2 in 1992-1998 and 2000, 3 in 1999, and ranged from 2-7 in 2001, 3-6 in 2002, and 2-5 in 2003.
during the period of hardwood removal and drought revealed a number of differences, again consistent with the hypothesis of drought as an important impact. During the period of hardwood removal and drought, juveniles weighed less \((t = 7.27, P < 0.0001)\), moved shorter distances between successive sightings within years \((t = 1.97, P = 0.058)\), and had a lower proportion of recruits \((X^2 = 11.61, P = 0.003, \text{Table 4})\). Adults also weighed less during the period of hardwood removal and drought than before it \((t = 6.95, P < 0.0001)\), but, unlike juveniles, they moved farther between successive sightings within years \((t = 2.14, P = 0.034, \text{Table 4})\).

**Discussion**

Land management practices at Tall Timbers appeared to influence our armadillo population. Effects of prescribed burning seemed weaker and transitory, but hardwood removal seemed to produce serious long-term effects. However, the confounding of hardwood removal with a period of severe drought makes it difficult to unambiguously identify the primary cause of changes we have documented. Drought can produce significant increases in mortality and consequent lower abundances in armadillo populations (McDonough and Loughry 1997b). While we can not discount the hypothesis...

<table>
<thead>
<tr>
<th></th>
<th>Before</th>
<th>During</th>
<th>After</th>
<th>Test</th>
<th>Pair-wise comparisons</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pairs c</td>
<td>0.216 (0.492)</td>
<td>0.397 (0.639)</td>
<td>0.234 (0.507)</td>
<td>F = 5.07</td>
<td>B, C</td>
</tr>
<tr>
<td>Litters d</td>
<td>0.348 (0.708)</td>
<td>0.182 (0.387)</td>
<td>0.136 (0.344)</td>
<td>F = 8.94</td>
<td>A, C</td>
</tr>
<tr>
<td>Proportion of juveniles e</td>
<td>126/393</td>
<td>37/350</td>
<td>48/240</td>
<td>x² = 51.12</td>
<td>A, B, C</td>
</tr>
<tr>
<td>Female lactational status f</td>
<td>67</td>
<td>53</td>
<td>45</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Definitely lactating</td>
<td>29</td>
<td>52</td>
<td>19</td>
<td>x² = 15.07</td>
<td>B, C</td>
</tr>
<tr>
<td>Possibly lactating</td>
<td>51</td>
<td>92</td>
<td>43</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Not lactating</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a Continuous data were analyzed with ANOVA and post-hoc Bonferroni-Dunn tests for pair-wise comparisons. Proportions were analyzed with chi-square tests, both for the entire data set and for individual pair-wise comparisons.

b Significant pair-wise comparisons indicated as: A = Before vs After, B = During vs After, and C = Before vs During.

c Number (±SD) of male–female reproductive pairs observed per number of sampling days; number of sampling days is the same as in Table 2.

d Number (±SD) of litters observed per number of sampling days.

e Number of juveniles captured versus total number of animals caught during each time period.

that logging had such pervasive effects that it impacted even those animals inhabiting unlogged areas, comparisons of animals in unlogged versus logged areas during the drought and of animals in unlogged areas before versus during the drought both support the hypothesis that drought was an important influence on our population (Table 4). Even so, for the following reasons, we believe the primary impact on our population was hardwood removal and that drought may have masked these effects during the period of logging. First, the drought ended by 2001, yet our population continued to decline even after weather conditions had returned to normal. Second, although animal weights did decline during hardwood removal (Table 2), we did not see the extreme emaciation observed in other armadillo populations experiencing drought conditions (McDonough and Loughry 1997b). Indeed, although somewhat smaller, the animals we captured during the drought still appeared relatively healthy. This was probably due to the fact that as a consequence of the drought, much of Lake Iamonia dried up, providing considerable additional area for foraging. This newly available habitat may have minimized negative impacts from the drought. In addition, this might explain why our population continued to decline after the drought was over. As lake levels returned to normal in 2001–2002, armadillos no longer were able to feed in the lake bottom. At this point the only ideal

Table 4. Characteristics (±SD) of juvenile and adult armadillos found in unlogged areas of Tall Timbers, Florida before (1992–1997) and during (1998–2000) the period of hardwood removal and drought and of armadillos found in logged areas during the period of hardwood removal and drought.

<table>
<thead>
<tr>
<th></th>
<th>Unlogged-before</th>
<th>Unlogged-during</th>
<th>Logged-during</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Juveniles</td>
<td>Adults</td>
<td>Juveniles</td>
</tr>
<tr>
<td>Weight (kg) a</td>
<td>1.37 (0.51)</td>
<td>4.12 (0.48)</td>
<td>1.75 (0.68)</td>
</tr>
<tr>
<td>n = 67</td>
<td>n = 106</td>
<td>n = 67</td>
<td>n = 109</td>
</tr>
<tr>
<td>Distance moved</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>within year (m)</td>
<td>73.32 (44.85)</td>
<td>101.32 (55.69)</td>
<td>58.41 (13.02)</td>
</tr>
<tr>
<td>n = 23</td>
<td>n = 41</td>
<td>n = 23</td>
<td>n = 10</td>
</tr>
<tr>
<td>Distance moved</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>between years (m)</td>
<td>254.35 (233.19)</td>
<td>197.32 (146.37)</td>
<td>693.63 (226.56)</td>
</tr>
<tr>
<td>n = 15</td>
<td>n = 40</td>
<td>n = 11</td>
<td>n = 8</td>
</tr>
<tr>
<td>Recruitment-retention</td>
<td>25/115</td>
<td>37/221</td>
<td>2/32</td>
</tr>
<tr>
<td>Number of individuals b</td>
<td>67/126</td>
<td>107/267</td>
<td>15/37</td>
</tr>
</tbody>
</table>

a With the exception of number of individuals, all variables defined in Table 2.

b Number of individuals of that age from that particular habitat type versus total number of individuals of that age captured during each time period.
habitat remaining in the study area was the small strip of hammock habitat along the lakefront. Presumably, this small area could not accommodate as many individuals and may have promoted further emigration out of our study site. This also could explain the increased sightings of adults in logged areas after completion of hardwood removal, as even animals remaining in the population might have been forced out into less desirable habitat in attempts to find sufficient food. Thus, to summarize, while drought may have been an important factor during the period of hardwood removal, it seems unlikely to explain the continued effects on our population since the completion of logging and the end of the drought. Consequently, we believe hardwood removal significantly impacted our population in long-lasting ways that may have been masked during the period of drought but continued to influence the population through the end of 2003.

Logging and the resulting fragmentation of forested habitats are well-known deleterious influences on many resident animal populations (Saunders et al. 1991, Andren 1994, Noss and Csuti 1997). At Tall Timbers hardwood removal coincided with a decline in armadillo abundance that persisted through 2003 (Figure 2). Given that sampling effort in 2001-2003 was more intensive (i.e., more time and more people in the field, see Figure 2) than in earlier years, we are convinced this decline was real. Armadillo abundances increased at the onset of logging (1998 and 1999, see Figure 2), probably just because animals were more conspicuous in the barren habitat produced by logging. However, over the ensuing years, the population declined steadily. Taken as a whole, the decline in abundance seems to be largely due to impacts on reproduction. Although data on reproductive behavior (Table 3) suggested that adult armadillos continued to mate successfully, data on numbers of litters found, the proportion of juveniles in the population, and the extent of juvenile recruitment all indicated that many of these reproductive attempts must have failed. After mating in summer, female nine-banded armadillos normally delay implantation of the fertilized egg until sometime in late autumn (Enders 1966). However, when stressed, females may delay implantation for considerably longer periods of time (e.g., up to 3 years in captivity, Storrs et al. 1989). Thus, some of the decline in offspring production associated with the onset of logging might have been caused by females delaying implantation until conditions improved.

Consistent with this hypothesis, we found a higher proportion of nonlactating females during logging (Table 3), suggesting that even though females continued to mate, they may not have given birth. Yet, it is possible that other factors, such as increases in juvenile mortality from increased conspicuousness and vulnerability to predators, inability of mothers to support the energetic demands of reproduction, or some other set of factors, also contributed to the decline in reproductive output we observed. Instead of reproductive failure, one also might explain the decline in juvenile abundance as the result of rapid early dispersal of young out of the study area. While possible, this hypothesis seems
unlikely as juveniles appear unfit for any long-distance movements during their first weeks above ground (C. M. McDonough and W. J. Loughry, unpublished data) and any attempt to do so would likely lead to death.

Partial support for the idea that reproductive failure might be caused by energetically stressed mothers comes from the finding that hardwood removal was associated with a decrease in weights of both juveniles and adults during and after logging. Part of this decline was undoubtedly due to the drought that occurred during the period of hardwood removal. However, this did not explain why weights continued to remain low in the years after hardwood removal was complete and the drought had ended. Armadillos forage for invertebrates in the soil and leaf litter (Redford 1985). Disturbance from logging, even after completion of hardwood removal, might have caused reduced foraging success by either limiting areas available for foraging or reducing prey availability within logged habitat. However, these hypotheses must remain speculative as we do not have detailed data on prey availabilities and individual foraging success necessary to fully test them.

Surprisingly, we found no support for the hypothesis that logging would precipitate increased ranging by armadillos as they tried to avoid disturbed areas. Distances moved, either within or between years, did not vary over the 3 time periods for juveniles or adults (Table 2). Notably, distances moved represented data from animals that remained within our study area, yet declining population numbers indicated many animals must have died or left the study site. If the latter, then these dispersing individuals would represent long-distance movements that we were unable to measure. If true, then logging would have induced wider ranging as predicted, just not among the core resident animals of our population, possibly because these individuals occupied areas least affected by logging.

In contrast to hardwood removal, fire appeared to generate weak and inconsistent effects on our population. Armadillos were first recorded at Tall Timbers in 1972 (Stevenson and Crawford 1974), and burning has been an important component of land management at Tall Timbers since at least the early 1950s (Stoddard 1962). Thus, armadillos at Tall Timbers have always been exposed to fire as a major feature of the environment. That the population remained and seemingly thrived up until the onset of hardwood removal suggests that fire represented no serious threat to the animals. Armadillos probably are able to avoid the immediate danger from fire by retreating to their burrows. Once fire has passed, there may be a temporary period when burned areas are unsuitable for foraging. Consistent with this expectation, in 4 of the 5 years for which we had data, adult armadillos did appear to avoid more recently burned habitat (Table 1). Juveniles probably did not because they typically do not range very far from their natal burrows (Loughry and McDonough 1998) and thus are likely to remain in the same area regardless of whether it was burned. Juveniles also presumably have less experience with and information about their environment and so may not avoid burned areas like adults. In any case, avoidance of burned areas appeared transitory and the overall impact of fire on our population was weak. These results were consistent with those from other studies that also have documented few, if any, serious consequences to animal populations from exposure to fire (e.g., Prada 2001, Moseley et al. 2003). However, fire may be more important in our population now than previously because fire, if used properly, may maintain less preferred habitats for armadillos by preventing reestablishment of hardwoods within logged areas.

Management implications

Nine-banded armadillos have the largest geographic range of any armadillo species, from northern Argentina to the southern United States (Taulman and Robbins 1996). Twenty other species
of armadillos are confined to specific regions of Latin America (Eisenberg 1989, Eisenberg and Redford 1999, Redford and Eisenberg 1992). In many of these areas, deforestation and slash-and-burn agriculture are serious human impacts on the environment. These practices are similar to what we have observed on a small scale at Tall Timbers. Thus, our data may have value in predicting how armadillos might respond to such practices in other parts of their range. Although important differences among armadillo taxa preclude sweeping generalizations, it does appear that for nine-banded armadillos, the more serious concern is with deforestation. Nine-banded armadillos appear able to adapt to fire with little long-term difficulty, but more permanent changes to the landscape by logging seem to have serious negative consequences. Data from armadillo populations in Latin America, experiencing the kinds of human disturbances we have described here, are now needed to determine the generality of our results.

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Literature cited

Environmental Systems Research Institute. 1999. ARC/INFO, version 3.2. Environmental Systems Research Institute, Redlands, California, USA.


Colleen McDonough (photo) received her B.S. in zoology from the University of Wisconsin and Ph.D. in animal behavior from the University of California, Davis. She has been on the faculty of the Department of Biology at Valdosta State University in Georgia since 1994 and is a full professor. She has collaborated with Colleen McDonough on field studies of nine-banded armadillos since 1990. She and Colleen have a 5-year-old daughter who so far has shown absolutely no interest in their work.

Current interests include assessing the extent and impact of leprosy infections in wild armadillo populations, chemical signaling, and comparative analyses of other armadillo species. W. J. (Jim) Loughry received his B.S. in biological sciences from the University of Pittsburgh and, in 1987, a Ph.D. in animal behavior from the University of California, Davis. During his time at Davis, his research focused on the antipredator behavior (snake mobbing and alarm calling) of ground squirrels, primarily black-tailed prairie dogs. He then spent 2 years as a National Institutes of Health post-doctoral fellow in ethology at the University of Tennessee, where he examined olfactory communication between mother and infant Mexican free-tailed bats. After 2 years in temporary positions, he landed a tenure-track position in the Department of Biology at Valdosta State University, where he is now a full professor. He has collaborated with Colleen McDonough on field studies of nine-banded armadillos since 1990. He and Colleen have a 5-year-old daughter who so far has shown absolutely no interest in their work.

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