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CHANGES IN OBSERVABILITY OF ADULT NINE-BANDED ARMADILLOS OVER THE SUMMER: OBSERVER EFFECT OR SEASONAL DECLINE?

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Abstract.—During a seven year (1992-1998) field study of nine-banded armadillos (Dasypus novemcinctus) in northern Florida, the number of adult armadillos observed per hour of observation declined significantly across the field season (mid June through late August). Such a decline could be due to a number of factors, including learned avoidance of the observers. As opposed to explanations based on seasonal changes, the observer effect hypothesis predicts that the number of armadillos observed per hour should decrease with increasing time in the field, regardless of when this time occurs. In 1999 we had an opportunity to test this prediction because our field season started and ended earlier (mid May through the end of July) than previously. We found a significant negative relationship between the number of adults observed per hour of observation and the number of days the population had been observed when data from all years were pooled, and in 4 of 7 field seasons when data from each year were analyzed separately. Most importantly, a significant negative relationship was obtained in 1999. Weather data and information on captures and resightings of individuals provided no evidence that the decline in 1999 was due to exceptional conditions occurring only that year. However, the number of adults observed per hour of observation was significantly higher in May of 1999 than in June of previous years, suggesting that there may be a longer-term seasonal decline in armadillo observability that is not due to an observer effect. To the extent that an observer effect occurs, it may amplify this long-term seasonal decline to produce the patterns we report here.

One perennial problem in field studies of wild animals is the extent to which the behavior of the animals is influenced by the presence of a human observer. For example, Isbell and Young (1993) showed that predators of vervet monkeys (*Cercopithecus aethiops*) shifted the timing of their attacks to periods when human observers of the monkeys were not present. In the present study, we examine the potential for an observer effect in a population of nine-banded armadillos (*Dasypus novemcinctus*).

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In a previous study (McDonough and Loughry 1997), the number of adult armadillos observed per hour of observation was significantly lower in August (toward the end of the field season) than in June (at the beginning of the field season). There are many possible explanations for this effect. For example, seasonal changes in weather patterns or prey abundance might alter the timing and extent of activity (Layne and Glover 1985, Inbar and Mayer 1999), or the animals might be just as active but less detectable as a result of vegetation growth over the summer. Alternatively, the decline might be associated with mating behavior (Mc-Donough 1997), with more adults being observed during the peak of the breeding season in June and early July (McDonough 2000) and declining subsequently. Finally, it is possible that, due to repeated exposure to the observers over the course of the summer, adult armadillos learn to avoid them. Unlike the other hypotheses, this last hypothesis predicts a decline in observations of adults with increasing days of observation, regardless of when those days occur. In this paper, we test this prediction by examining data from our 1999 field season, which began and ended earlier than normal (mid May to the end of July). If seasonal effects drive the decline in observations of adults, less of an effect should be observed in 1999 because the field season ended before the decline becomes pronounced. On the other hand, if learned avoidance is an important factor, then the decline should still occur because the animals had the same amount of exposure to human observers as in previous years.

Methods

Data were collected on the nine-banded armadillos inhabiting Tall Timbers Research Station, Leon County, Florida. With the exception of 1996, this population has been studied each summer since 1992 (seven field seasons total). Basic procedures are described in detail elsewhere (McDonough and Loughry 1997, Loughry and McDonough 1998a, McDonough et al. 2000). Briefly, we censused the population each night by walking or driving along roads on the property. We attempted to capture all unmarked armadillos observed during these censuses by using large dip nets attached to 1.5 or 2 m poles. Once captured, animals were weighed, measured, and marked for permanent identification with a passive induced transponder (PIT) tag injected under the skin and for long-range identification with reflective tape glued to the carapace. In addition, an ear notcher was used to obtain small tissue samples for genetic studies. Once captured and marked, animals were not recaught again during the year unless the reflective tape had worn off and they needed to be remarked.

Data from these censuses were used to calculate the number of adult (≥1 year old) and juvenile armadillos observed per hour of observation each day. Unmarked animals observed but not captured were assigned to age groups on the basis of body size (McDonough 1994, Loughry and McDonough 1996, McDonough et al. 1998). Resightings of the same individual on the same day were not counted to avoid pseudoreplication.

We used linear regression (Statview 4.01) to examine the relationship between the number of adults seen per hour of observation and the number of days of observation from the beginning of the field season, using both all hours of observation each day (8:00-24:00), and just nighttime hours (16:00-24:00), when adults are usually most ac-

tive (McDonough and Loughry 1997). We followed Brunig and Kintz (1977) in calculating the statistical significance of differences between regression coefficients.

To further examine potential evidence for an observer effect, we looked at the patterns of captures and resightings of individual armadillos in each year of the study. We first tallied the total number of individuals observed each year, then determined the number of individuals from this total that were (a) never seen again that year or in any subsequent year; (b) never seen again that year but were observed in some subsequent year; and (c) resighted during the same field season. For this last group we calculated the average number of resights per individual and the average number of days between successive sightings. These data were analyzed for age and sex differences in resight patterns with a two-way ANOVA (Statview 4.01).

It is possible that any pattern of armadillo observations obtained in 1999 could be due to exceptional circumstances making that year unique. We attempted to evaluate this possibility in two ways. First, we compiled our resight data by month for each year of the study. We used these data to compare patterns obtained in 1999 with those observed from 1992-1998, reasoning that, if armadillos responded to us as they had in previous years, then data for May of 1999 should be similar to that from June of 1992-1998, June of 1999 should mirror data from July, 1992-1998, and so on. Second, data from the Tall Timbers weather station were used to compare climatic conditions between years. Based on previous analyses of the relationship between weather conditions and armadillo activity patterns (McDonough and Loughry 1997), daily minimum and maximum air temperature, and amount of precipitation were selected as the critical variables for comparison. In cases where weather station data were not available, we substituted observations from the Tallahassee Regional Airport (National Climatic Data Center database), located approximately 25 km south of Tall Timbers. Using t-tests, we compared data from each month of the 1999 field season (May, June, and July) with the pooled data from the corresponding month in 1992-1998 (excluding 1996).

Seasonal effects might still be invoked to explain a significant decline in armadillo observability in 1999 if such a decline includes more than just the June to August period sampled previously (T. Engstrom pers. comm.). For example, if the number of adult armadillos observed per hour of observation was highest in May and declined in each subsequent month of the summer, then data from 1992-1998 would represent a sampling of the latter part of this decline, while data from 1999 represent a sampling of the earlier component. In order for this hypothesis to be valid, numbers of adult armadillos observed per hour in May must be higher than numbers observed later (e.g., June). We tested this prediction in two ways. First, we used a paired *t*-test to compare numbers of armadillos observed per hour of observation for each of the first 17 days of the 1999 field season (which encompassed sampling in May) versus the first 17 days of sampling in 1992-1998 (which encompassed sampling in June; data were averaged across the years 1992-1998 for this comparison). Second, because of variable starting dates in the field each year (Table 1) a paired comparison required elimination of some later sampling dates that still occurred within the appropriate month (e.g., days 18-20 of 1999 occurred in May but occurred in June or July of 1992-1998). Thus, to include all appropriate sampling dates, we used an unpaired *t*-test to compare average numbers of armadillos observed per hour of observation in May of 1999 with numbers observed in June of 1992-1998.

In what follows, means are reported ±SD.

RESULTS

Consistent with previous analyses (McDonough and Loughry 1997), when data from all years (1992-1999) were analyzed, there was a significant decline in the number of adults observed per hour of ob-

Year	Starting and ending dates	Number of observation days	r (Nights only)	Years different	r (All hours)	Years different
1992	15 June-29August	61 (60)	-0.37**	none	-0.26*	1994
1993	21 May-18 August	45 (43)	-0.34*	none	-0.22	1994
1994	14 June-26 August	44 (38)	-0.52^{***}	1998	-0.72^{***}	all but 1999
1995	19 June-23 August	49 (49)	-0.25	none	-0.22	1994
1997	16 June-15 August	50 (48)	-0.27	none	-0.21	1994
1998	15 May-22 August	52(48)	-0.04	1994, 1999	-0.16	1994, 1999
1999	10 May-30 July	63(62)	-0.55***	1998	-0.50***	1998

Table 1. Results of regression analyses of the numbers of adult nine-banded armadillos observed per hour of observation and the number of days the population was observed for each year of the study.

*P < 0.05, **P < 0.01, ***P < 0.001; sampling in May consisted of 1 day each in 1993 and 1998, and 20 days in 1999 (regular sampling began on 16 June in 1993 and 15 June in 1998). For number of observation days, sample sizes for number of nighttime observations are given parenthetically. Years different column indicates which regression coefficients from other years differed significantly from those of the selected year.

servation with increasing numbers of days in the field, regardless of whether all hours of observation were included (r = -0.23, P < 0.001, n = 362, Fig. 1) or just those from the night (r = -0.22, P < 0.0001, n = 348). The same results were obtained when only data from 1992 through 1998 were used (for all hours of observation, r = -0.19, P < 0.008, n = 299; for nights only, r = -0.18, P < 0.002, n = 286, Fig. 1). Also consistent with our earlier analyses, observations of juveniles did not covary with number of days of observation (pooled data from all years and all hours of observation, r = 0.05, P = 0.37, n = 362).

Separate examination of each field season showed a significant decline in numbers of adult armadillos observed per hour with increasing numbers of observation days in 3 of 7 years when all hours of observation were included (Table 1), and in 4 of 7 years when only nighttime hours were included (Table 1; the value for 1997 is marginally significant, P < 0.07). Most importantly, a highly significant negative relationship between observations of adults and number of days of observation was found in 1999 (Table 1).

In general, regression values were similar between years (Table 1), although the relationship in 1994 was very different from that in any other year when all hours of observation were included, but less so when just nighttime hours were examined. The regression coefficients obtained in 1999 were significantly different from those obtained using pooled data from 1992-1998 (all hours, Z = 2.52, P = 0.012; nights only, Z = 3.05, P = 0.002). However, separate comparisons of 1999 with each of the other field seasons revealed significant differences with 1998 only (Table 1).

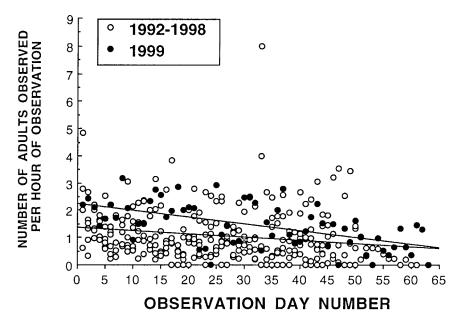


Figure 1. Relationship between number of adult armadillos observed per hour of observation and the number of days the armadillos had been observed. The upper regression line was generated using data from 1999 only, the lower line used data from 1992-1998. Both lines were calculated using data from all hours of observation (day + night) each day. See the text and Table 1 for the statistical results of these analyses.

In each field season, $\geq 46.7\%$ of the animals observed were only seen once (combining the third and fourth columns of Table 2). Even those that were resighted within the same field season averaged only 2.02 ± 1.57 additional sightings, with an interval of 15.70 ± 12.98 days between successive sightings (Table 2; pooled across all years and all individuals). Pooled across all years, the average number of resights per individual did not differ between age classes or between males and females (two-way ANOVA, P = 0.50 for age main effect and P = 0.82 for sex main effect, age by sex interaction was also not significant, P = 0.23). However, there was a significant age, but not sex, difference in the average number of days between successive sightings (P = 0.0004 for age main effect; P = 0.66 for sex main effect; P = 0.97 for age by sex interaction).

Patterns of observations in 1999 were similar to those in 1992-1998 (Table 3). The distribution of captures for individuals that were subsequently resigned that year as well as the total number of individuals observed per month were not significantly different between 1999 and 1992-1998 ($\chi^2 = 2.61$, P = 0.27 for new captures, $\chi^2 = 0.37$, P = 0.83 for total individuals). The average number of resignts per individual and

	Number	Number never seen again	Number not resighted until following vear(s)	Number withi	Number resighted within year	Ave number (per inc	Average number of resights per individual	Ave numbe: between	Average number of days between resights
Year	captured	(% of total)	(% of total)	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
1992	72	23 (38.9)	20 (27.8)	13	11	2.31	2.18	24.48	5.87
1993	94	27(28.7)	28(29.8)	28	11	1.57	2.27	16.53	12.94
1994	49	12 (24.5)	27 (55.1)	7	က	1.86	1.00	20.07	3.33
1995	136	66(48.5)	32(23.5)	32	9	1.63	2.50	15.00	16.11
1997	112	39(34.8)	44 (39.3)	27	2	1.44	1.00	22.43	2.50
1998	225	67 (29.8)	38(16.9)	109	11	2.28	1.73	15.48	5.30
1999	170	I	I	78	0	2.17		15.83	
Data fo:	r adults incluc	les yearlings as well.	Data for adults includes yearlings as well. Number captured excludes animals found dead	cludes anima	als found dead.				

Table 2. Capture and resight data for armadillos at Tall Timbers each year of the study.

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			Month 1		Moi	Month 2		Moi	Month 3
Year	R	Number of resights	Days between resights	n n	Number of resights	Days between resights	u u	Number of resights	Number of Days between resights resights
1992	6 (16)	2.83	25.65	6(23)	2.00	24.72	1 (18)	1.00	16.00
1993	23(39)	1.61	16.89	2(42)	1.00	30.00	3(21)	1.67	4.83
1994	6(34)	2.00	21.58	1(6)	1.00	11.00	0 (7)	I	Ι
1995	19(36)	1.79	16.17	12(63)	1.42	13.97	1(18)	1.00	5.00
1997	18 (49)	1.44	27.71	9(51)	1.44	11.86	0(17)		Ι
1998	62(98)	2.36	15.29	39(150)	2.08	11.36	0(46)	I	I
1999	58(88)	2.40	15.99	19(98)	1.53	15.84	1(38)	1.00	6.00
For year Sample total nun seen tha	For years 1992-1998, n Sample sizes refer to th total number of live an seen that month but n	month 1 = June the number of ii nimals observed not again during	For years 1992-1998, month 1 = June, month 2 = July, and month 3 = August. For 1999, month 1 = May, month 2 = June, and month 3 = July. Sample sizes refer to the number of individuals first observed during each month that were subsequently resighted during the field season. The total number of live animals observed each month (which includes resightings of animals caught earlier in the field season and animals first seen that month but not again during that year) is given parenthetically.	and month 3 served durir ich includes en parenthet	= August. For ig each month resightings of <i>i</i> cically.	1999, month 1 = 1 chat were subsequ animals caught ea	May, month lently resigh urlier in the	2 = June, and n ted during the field season and	nonth 3 = July. field season. The 1 animals first

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average number of days between sightings also did not differ between 1999 and 1992-1998 for comparable months (e.g., month 1 = May of 1999 versus June of 1992-1998; *t*-tests for all comparisons, all P > 0.15; no comparisons were made for month 3 because of small sample sizes, see Table 3).

There was little indication of unusual weather conditions in 1999. Pooled across months, there were no differences in weather conditions in May-July 1999 versus May-July of 1992-1998 (*t*-tests, all P > 0.10; see Table 4). However, month-by-month comparisons showed that June and July of 1999 had significantly higher minimum air temperatures than in previous years (Table 4). Weather conditions did not differ significantly between 1999 and 1992-1998 in any other comparison of corresponding months (Table 4).

Finally, there was evidence of a longer term seasonal decline in armadillo observability. The number of adult armadillos observed per hour of observation was significantly higher in May of 1999 than in June of 1992-1998 in a paired comparison of the first 17 days of observation (1999 mean = 2.03 ± 0.55 , 1992-1998 mean = 1.27 ± 0.41 ; t = 4.80, P = 0.0002) and in an unpaired comparison of all sampling days in May of 1999 versus all days of sampling in June of 1992-1998 (1999 mean = 2.07 ± 0.54 , n = 20; 1992-1998 mean = 1.35 ± 0.74 , n = 104; t = 4.16, P = 0.0001).

	1992-1998	1999	P^*
May			
Maximum temperature (°C)	30.15(3.09)	30.20 (2.18)	0.93
Minimum temperature (°C)	16.14(3.49)	16.42(3.61)	0.69
Precipitation (cm)	0.31(1.22)	0.57~(1.92)	0.33
n	182	31	
June			
Maximum temperature (°C)	32.38(3.32)	31.54(1.60)	0.17
Minimum temperature (°C)	20.54(2.20)	21.69(1.07)	0.006
Precipitation (cm)	0.51(1.21)	0.63(1.21)	0.61
n	180	30	
July			
Maximum temperature (°C)	33.50(2.08)	33.33(2.40)	0.69
Minimum temperature (°C)	22.24(1.27)	22.85(1.04)	0.012
Precipitation (cm)	0.68(1.44)	0.60 (1.04)	0.78
n	186	31	

Table 4. Average $(\pm$ SD) weather conditions at Tall Timbers during May, June, and July 1992-1998 and 1999.

*t-tests, data for 4 days in May of 1992-1998 were unavailable.

DISCUSSION

There are many possible explanations for the decline in the number of adult nine-banded armadillos observed per hour of observation over the course of the summer at our study site. The results presented here provide some support for an observer effect such that adults learn to avoid observers, as well as for a longer term seasonal decline in armadillo observability. It seems likely that both of these factors, and possibly others we have yet to identify, work together to generate the patterns we report. For example, to the extent that an observer effect occurs, it may only amplify the underlying seasonal trend that is already present.

It is perhaps not surprising that we found some evidence of an observer effect. As described in the methods, our capturing and marking procedures undoubtedly stress the animals. We may even unintentionally generate stress on individuals not subject to capture by making noise as we move around during our censuses, perhaps mimicking the sounds of an approaching predator and causing the animals to flee the area. It is logical to assume the animals might learn to avoid such negative stimuli. What is not clear is how much exposure is required to generate this effect. While we are routinely present in the study site during the summer, we do not encounter the same individuals night after night (Table 2; Loughry and McDonough 1998b). Thus it seems that, if avoidance occurs, it can be generated with infrequent human contact. However, it also possible that extensive exposure to humans may eliminate any learned avoidance. The dramatic range expansion of D. novemcinctus in the last 150 years (Humphrey 1974, Taulman and Robbins 1996), which includes many areas with high human density, suggests that this species is highly adaptable and may habituate to the presence of human beings. Nonetheless, our data showed that nearly half the animals observed in any given year were only seen once. These animals could not all have been transients that were captured while residing temporarily within our study site because about half of them were seen again in a subsequent year, typically very close to where they were observed initially (Loughry and McDonough 1998b). While we did not do so for our analyses, factoring in these individuals would greatly lengthen our estimates of days between successive sightings, further supporting the notion that human contact may lead to avoidance of human observers. Armadillos might be able to avoid human observers by being active at times of day when observers are not present, or by shifting activity to parts of the home range not routinely sampled by us. This latter possibility might help explain the age difference in number of days between successive sightings. Juveniles remain within a very small area during their first summer above ground (Loughry and McDonough 1998b), so they may have fewer options for relocation and, thus, may be found again more quickly.

One could argue that the case for an observer effect in our population is weak because it is based on the outcome of a single field season. We agree that additional years of sampling, on the same schedule as in 1999, are required to confirm that such an effect occurs. Nonetheless, it seems unlikely that data obtained in 1999 were due to unusual conditions making that year unique. Weather conditions (Table 4) were similar in 1999 to those seen in earlier years. Of particular interest with regard to an observer effect, analyses of data in Table 3 suggested that patterns of adult captures and resightings in 1999 were similar to those obtained in earlier years, but advanced by one month. Thus, data from May of 1999 were similar to those obtained in June of 1992-1998, June of 1999 was similar to July of 1992-1998 and so on. It is difficult to explain how this could occur if seasonal effects alone generated changes in armadillo observability, because one must argue that conditions in 1999 mimicked those that normally occur one month later. We found little evidence of this, although daily minimum air temperatures were significantly higher in June and July of 1999 than in previous years (Table 4). One might argue that these warmer temperatures represent conditions normally occurring later in the summer. While this could be true, we think it is unlikely to explain the results we obtained in 1999 because, in an earlier analysis (McDonough and Loughry 1997), armadillo activity was positively correlated with higher daily minimum temperatures. Based on this relationship, no decline in observations of armadillos in July of 1999 is predicted.

Weather and resight data suggest 1999 was not an unusual year, but conditions did vary between field seasons and may have contributed to the patterns we report here. For example, regression coefficients for 1994 (Table 1) were significantly different from those in every other year (when all hours of observation were included) probably because two tropical storms passed through Tall Timbers that year, resulting in some flooding of our study site and probably driving many animals out of our sampling areas (McDonough and Loughry 1997). Thus, any observer effect occurring in this year would have been greatly enhanced by the scarcity of animals due to flooding. On the other hand, 1998 exhibited the weakest relationship between number of days of observation and number of armadillos sighted per hour. We observed more animals in 1998 than in any other year (Tables 2 and 3), probably because Tall Timbers initiated a hardwood removal program that year that may have disturbed the animals and forced them into open areas where we could see them more easily. In this case, any observer effect may have been overwhelmed by the disruptions associated with timber removal.

Any discussion of an observer effect in our population must be tempered by the finding that armadillo observability was significantly higher in May of 1999 than in June of 1992-1998. Thus, it seems likely that there is a long-term seasonal decline in observability that lasts at least from May through August. Whether this pattern extends beyond these months will require sampling earlier and later in the year. Causes for this long-term seasonal decline are not obvious. Based on observations of mating activity (McDonough 2000), emergence of young (Loughry and McDonough 1998b), and annual cycles of activity (Layne and Glover 1985; Inbar and Mayer 1999), one might expect a peak in adult observability in June or early July, but not May. Alternatively, because armadillos do not hibernate and thus must forage year-round, one might expect that adults are equally active throughout the year but that observability changes due to changes in the conspicuousness of individuals (e.g., by foraging for less time or later at night, remaining in thick vegetation, etc.). Our data do not allow us to distinguish among these alternatives and further work will be required to identify the factors that produce the summer-long decline we have documented.

To the extent that adult armadillos do exhibit an observer effect, researchers may need to exercise some caution when developing sampling regimes for this species. Care should be taken to vary the times during the day when observers are present and either limit the exposure of each animal to human contact (to minimize the possibility of avoidance) or increase exposure while minimizing stress (to maximize the possibility of habituation). However, further work is required to more fully describe changes in adult observability over the course of the year so that the effects of seasonal changes and exposure to human observers might be more fully disentangled.

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