

Spatial Ecology and Survivorship of Resident and Translocated Hognose Snakes (*Heterodon platirhinos*)

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ABSTRACT.—Movements and survivorship of eight resident and eight translocated adult *Heterodon platirhinos* were monitored daily with radiotelemetry during the activity seasons (15 April–15 October) of 1992 to 1994 in upland open forest habitat. Hognose snakes were diurnally active and used a variety of open and edge microhabitats with grassy or leafy groundcover. Resident snakes were active on about 57% of days but some were inactive for extended periods (up to 68 d) in midsummer. Residents confined their movements within large (\bar{x} = 50 ha), well-defined home ranges which, for individuals, remained similar in size and location from year-to-year. Movements of both resident and translocated snakes averaged approximately 120 m/d, but movements of residents were confined to home ranges whereas those of translocated snakes were not so confined. Compared to residents, translocated snakes exhibited a 6× greater variance in distance of daily movements and made most of the long (>400 m/d), unidirectional movements. Resident snakes survived, on average, more than 3× longer (\bar{x} = 122 d) than translocated snakes (\bar{x} = 36 d) within the 184 d annual activity season.

Despite generally having low rates of success (<50% for birds and mammals, Griffith et al., 1989; <25% for amphibians and reptiles, Dodd and Seigel, 1991), translocation programs have become an established and widely used wildlife management strategy for a variety of animals (e.g., Boyer and Brown, 1988; Griffith et al., 1989; Dodd, 1993; Wilson and Price, 1994). For many non-game species, such as most reptiles, effective management strategies are poorly known and often based on nonbiological criteria (Dodd and Seigel, 1991; Scott and Seigel, 1992). In particular, rates of success for translocation strategies have been lower for non-game species than for game species (Griffith et al., 1989), and its efficacy for reptiles, including snakes, is largely untested and unknown (Reinert, 1991; Dodd, 1993; Reinert and Ruppert, 1999). The fact that snakes move in a predictable manner (Gibbons and Semlitsch, 1987; Slip and Shine, 1988; Plummer, 1990; Durner and Gates, 1993; Secor, 1994; Secor and Nagy, 1994; Plummer and Congdon, 1994; Shine and Fitzgerald, 1996), requiring familiarity with an area, suggests that translocation to unfamiliar areas could disrupt normal movements. Indeed, a few telemetric studies have reported erratic, long-distance movements by individual snakes following displacement from their home ranges (e.g., Fitch and Shirer, 1971; Landreth, 1973; Galligan and Dunson, 1979), but only one study to date was designed to test for long-term behavioral and survival differences between resident and translocated snakes (Reinert and Ruppert, 1999).

The greatest constraint in conservation planning for snakes is the fundamental lack of basic biological information for most species (Dodd, 1987, 1993; Reinert, 1993), and implementing a conservation program without regard to or in ignorance of the specific biological constraints on a given species has little chance of success (Dodd and Seigel, 1991; Scott and Seigel, 1992). For example, although a thorough knowledge of the use of space is important to understanding the ecology of any mobile species (Brown and Orians, 1970), our knowledge of spatial use for most snake species is sparse (Reinert, 1993) and our interpretations may vary with geography (Shine, 1987; Plummer and Congdon, 1994) and methodology (Gregory et al., 1987).

The hognose snake, *Heterodon platirhinos*, is a relatively poorly-studied species for which there is some concern for its overall conservation status (Dodd, 1987). Based on mark-recapture techniques, Platt (1969) provided an account of the spatial ecology of *H. platirhinos* near the species' western range margin. In this study, we use radiotelemetry to provide an account of the species' spatial ecology in a more central portion of its range. In addition, due to the prominence of translocation programs as a management strategy for many animals, we compare spatial ecology and survivorship of resident adult *H. platirhinos* with those of non-resident adult *H. platirhinos* which were captured offsite and translocated to the study area. Because the lowest rates of translocation success have been with endangered, threatened, or sensitive species, the efficacy of translocation for a snake species should be studied before it approaches a last resort (Griffith et al., 1989).

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MATERIALS AND METHODS

The approximate 250 ha study area was located in the easternmost part of the Arkansas River Valley subdivision of the Ouachita Mountain region of Arkansas (Foti, 1974) and bordered the Little Red River approximately 5 km N of Searcy in White Co. (35°15'N, 91°44'W). Topography was rolling to hilly and varied in elevation from approximately 60–120 m above sea level. Soils were loose, sandy, thin, and often rocky. The stunted vegetation of the xeric higher areas was upland deciduous woodland whereas that of the more mesic lower areas was upland deciduous forest (Foti et al., 1994). Common trees in xeric areas included oaks, *Quercus stellata* and *Q. marilandica*, hickory, *Carya texana*, and juniper, *Juniperus virginiana*. In mesic areas, other trees, such as sweetgum, *Liquidambar styraciflua*, blackgum, *Nyssa sylvatica*, and sycamore, *Platanus occidentalis*, also contributed to the forest canopy. Natural small grassy openings were common, especially in the xeric areas. Other openings included man-made clearings such as primitive roads, trails, pipeline and powerline right-of-ways, abandoned fencerows, pastures, mowed fields, oldfields, and a large quarry.

Transmitters (AVM SM-1 or Telonics CHP-2P) were implanted into recently captured *H. platirhinos* following the procedures of Reinert (1992). Each snake was assumed to be an adult based on Platt's (1969) minimum snout-vent length (SVL) at maturity (males, 45 cm; females, 50 cm). Transmitter mass was approximately 2–6% of snake body mass. Resident snakes were released at their point of capture the day after implantation. Translocated snakes were captured offsite from various localities from 8 to 40 km distant, implanted, transported to a central portion of the study area, and released within 5 d of capture in habitat considered to be optimal (grassy clearings) based on data collected from resident snakes. With few exceptions, each snake was located once each day (one "radio-day") during the 184 d activity season (15 April to 15 October). At each location, we recorded compass direction and distance from known landmarks, time, and climatic conditions. We also recorded habitat (forest, roadside, forest clearing, field), groundcover (grass, leaves, herbaceous, bare dirt), and behavior (moving, immobile and hidden, basking). Locations were plotted and digitized onto a recent (1990) aerial photograph of the study area (US Department of Agriculture, Agricultural Stabilization and Conservation Service; scale 1 mm:7.92 m). Snakes were recorded as active on a given day if their location was at least 5 m from the previous day's location. Distance moved each day was calculated as the linear distance between

successive daily locations. We handled snakes only when they were initially collected and for periodic transmitter battery replacements (about every five months). We assumed that a snake had been depredated if we found the transmitter and either partial or no remains of the snake.

We used McPAAL ver. 1.22 (Michael Stuwe, Smithsonian Institution) to calculate minimum convex polygon (MCP) home ranges, recognized by Gregory et al. (1987) as the method of choice for snakes. We excluded locations made on inactive days (i.e., days when distance moved was 0) because such locations were highly dependent on a previous choice (White and Garrott, 1990) and provided no new information for home range calculation. Excluding such locations has no effect on the size or shape of MCP home range because they are contained within the convex polygon drawn around the outermost locations. The procedure of excluding days with no movement has an advantage over including all consecutive days because it provides a more satisfactory answer to the question of how many data points are needed to estimate a snake's home range. The important question becomes one of how many movements are needed rather than how many days are needed. This focus should be more useful with animals such as snakes which can be unpredictably inactive for a high percentage of days as well as for extended periods. We calculated home ranges for the entire activity season (annual home range) for individuals having a minimum of 30 actively-chosen locations and also for time series analysis of successive 20 active-day periods. We used SYSTAT (SYSTAT, 1992) for statistical data analysis and the Trent-Rongstad estimate (Krebs, 1989) for survival analysis. Confidence intervals for Trent-Rongstad survivorship estimates were calculated using the Poisson approximation to the binomial using Appendix 1.2 from Krebs (1989). A one-tailed binomial test (Zar, 1996) was used to test if the Trent-Rongstad survival rate of translocated snakes was less than that of resident snakes. We used a Mann-Whitney test to compare periods of survivorship within years. To overcome pseudoreplication in hypothesis testing across years, survival data from individual snakes tracked for more than one season were pooled across years, log-transformed, and tested with a *t*-test. Statistical significance was determined at an alpha level of 0.05. Unless otherwise stated, means are reported with their standard errors and sample sizes.

RESULTS

The results are based on monitoring a total of 1351 radio-days on eight individual resident snakes and 355 radio-days on eight individual translocated snakes during the activity season,

which defined here, was the 184 d period extending from 15 April through 15 October (Table 1). The actual length of the activity season varied from year to year depending primarily on air temperature. From mid-October through mid-December and mid-March through mid-April, snakes often emerged from hibernation to bask and sometimes moved short distances during extended warm periods.

Over the course of the study, no evidence of infection from surgery was observed, and the one known gravid female successfully oviposited. Six resident snakes gained an average of $4.7 \pm 4.7\%$ in body mass (range -13% to 21%) whereas three translocated snakes gained $\bar{x} = 29 \pm 5.8\%$ (range 22.6% to 41%). Body mass change data on individuals, especially translocated snakes, were limited due to high predation rates.

Resident *H. platirhinos* were unimodally active during the daylight hours (Fig. 1), were moving 18.8% of the times when located, and were active on an average of $57 \pm 4\%$ of days. Possible nocturnal activity was examined during June through August by comparing the behavior and location of individual residents in late evening with their behavior and location early the next morning. In each of 31 cases, the location and behavior (inactive and coiled under grass or surface litter) recorded for late evening and subsequent early morning observations were identical, suggesting that there was little extensive nocturnal activity.

Total days of inactivity for residents averaged $43 \pm 4\%$, over half of which ($24 \pm 3\%$) was associated with ecdysis. Inactive days not related to ecdysis were often associated with either cool, overcast days or extended hot, dry periods. For example, male no. 6 was inactive on 68 consecutive days from 7 July to 12 September 1993. The only activity recorded during this time was a 32 m movement on 17 August and a return to the original aestivation site three days later. This same snake was again largely inactive on 42 consecutive days from 3 July to 13 Aug the following year. During this time, activity occurred on only five days for a total movement of only 118 m. Compared to the five resident males monitored, three resident females tended to exhibit more constant levels of activity throughout the season (Fig. 2).

Resident snakes were most often (68.3% of locations) associated with grass or grassy areas containing various amounts of leaf litter, herbs, and shrubs. The most characteristic microhabitat for an inactive snake was to be hidden under, and coiled at, the base of a clump of grass, while that for an active snake was to be crawling through grass. The strong association with grass groundcover was reflected in choice of macro-

habitat. Preferred macrohabitats were sufficiently open to permit grass growth (i.e., open forest, field, oldfield, clearing, road or trail; collectively 91.0% of locations). An apparent exception was that of no. 8, a phenotypically distinct (brightly-colored, vividly-blotched) male who spent 17.0% of his radio-days in closed forest compared to only 6.3% for all other snakes combined. Unlike many snakes, resident *H. platirhinos* rarely (0.17% of locations) took refuge under surface objects such as logs, rocks, or human-related litter (cardboard, plywood, etc.), despite an abundance of such microhabitats on the study area. Likewise, snakes rarely (0.50% of locations) took refuge in mammal burrows and never took refuge in self-constructed burrows as commonly occurs in Kansas (Platt, 1969).

Resident snakes moved an average of 119 ± 4 m on each day of activity with low among snake variation in movement (Table 2). Individuals repeatedly visited sites occupied previously, both within and between years, and used similar paths to move between sites. Five males tended to move more in early and late season than in midseason whereas three females tended to move less in early and late season than in midseason (Fig. 2).

Because we were in the field every day during the activity season, we were able to identify obvious temporary sojourns which seemed not to be normal day-to-day home range movements (Brown and Orians, 1970) and exclude them from calculations. For example, residents male no. 11 and female no. 1 overwintered in the quarry at the SE corner of the study area, both at the periphery of their primarily non-overlapping respective home ranges. Two weeks after emergence, the female moved 600 m unidirectionally westward through the central portion of her home range. The following day, male no. 11 likewise moved unidirectionally westward, closely adhering to the female's trail. After locating the female, the male mated with her (Plummer and Mills, 1996), shed, and quickly retraced his westward path back to his home range, which extended from the quarry in the opposite direction (northeast), and occupied this area for the remainder of the year. If the westward mating sojourn was included in the calculation of his home range, the total home range area would have been increased by about 70% (i.e., 111.2 ha vs. 65.5 ha, Table 1).

Home range locations overlapped extensively among individual resident *H. platirhinos*. Home ranges varied in area from 21.4–72.8 ha and averaged 50.2 ± 6.4 ha (Tables 1, 2; Fig. 3). Whether these large, total season home ranges resulted from individual snakes shifting between successive non-overlapping smaller areas was tested by superimposing successive 20 active-day

TABLE 1. Times of monitoring, activity, daily movement (excluding days of no movement), minimum convex polygon annual home range (calculated for snakes with a minimum number of 30 locations), period of survivorship, and fates of eight resident and eight translocated adult *Heterodon platirhinos* during the 184-day activity season (15 April–15 October) by year. "Unknown" indicates the disappearance of a snake to an unknown cause (likely either transmitter failure or bird depredation). Means are accomplished by their standard deviations.

No.	Sex	SVL (cm)	Yr	Dates monitored	% days act.	Movement (m/d)	Home range (ha)	Survival (d)	Fate
Residents									
1	F	65.5	92	0415-1015	54	131 ± 110	58.6	183	hibernated
1	F	70.0	93	0418-1008	55	122 ± 109	59.9	176	unknown (bird dep.?)
5	M	56.0	92	0612-0710	62	106 ± 8	—	29	depredated (mammal)
6	M	57.0	93	0415-1015	41	109 ± 116	72.8	183	hibernated
6	M	59.0	94	0415-1015	51	125 ± 104	26.6	183	hibernated
7	F	61.0	93	0506-0703	66	112 ± 135	50.5	59	depredated (bird)
8	M	48.0	93	0422-1015	55	133 ± 97	46.2	175	hibernated
8	M	50.5	94	0415-0826	45	112 ± 106	21.4	134	depredated (bird)
9	F	63.0	93	0502-0603	85	111 ± 43	—	33	depredated (mammal)
11	M	47.5	93	0429-1015	64	109 ± 117	65.5	168	hibernated/froze?
13	M	46.0	94	0415-0508	54	142 ± 189	—	24	depredated (bird)
Nonresidents									
2	F	76.0	92	0513-0625	63	221 ± 238	—	44	left study area?
3	F	61.0	92	0513-5016	75	31 ± 31	—	3	depredated (mammal)
4	F	73.0	92	0525-0624	6	29 ± 5	—	30	unknown
10	F	68.0	93	0702-1015	58	162 ± 409	—	75	hibernated
10	F	70.0	94	0415-0429	67	146 ± 93	—	15	depredated (fish)
12	F	73.0	92	0521-0712	57	206 ± 308	—	53	unknown
14	M	60.5	94	0523-0704	26	96 ± 120	—	43	depredated (mammal)
15	F	58.5	94	0708-0821	44	106 ± 65	—	45	depredated (bird)
16	M	56.5	94	0710-0724	27	81 ± 57	—	15	died (unknown cause)

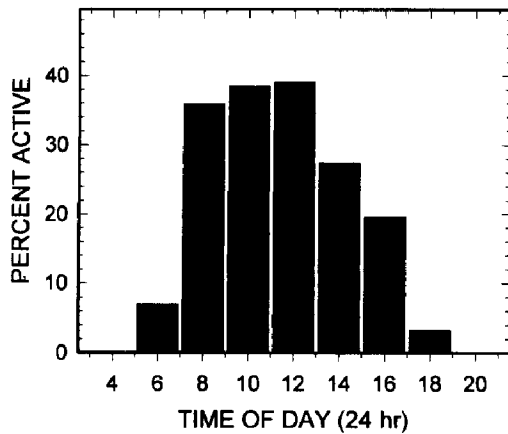


FIG. 1. Percent of pooled locations of eight resident *Heterodon platirhinos* that were active when located by time during the activity season (15 April–15 October).

home ranges for each of six individuals. A pattern of broadly overlapping areas typically resulted (Fig. 4). "Combined" home range, calculated as the sum of the non-overlapping portions of these smaller areas (Madsen 1984; Johnson, 1995), averaged 41.9 ± 7.1 ha, a value equal to 89.1% of the single annual home range estimate for the six snakes.

Home range size, location, and utilization were often remarkably similar for individual resident snakes in successive years (Figs. 3–5). An apparent exception was no. 6 which exhibited between-year differences in home range size, location, and utilization (Fig. 6). However, time-series analysis suggested that the between-year differences largely resulted from a shift in home range location in May 1993 after overwintering in the quarry. Indeed, movements from June through October of 1993 compared to movements throughout the entire year of 1994 showed a mostly typical pattern of comparable home range size, location, and utilization between years (Fig. 6; 1993—29 ha, 1994—27 ha; 67% overlap in location between years).

Translocated snakes neither confined their movements to a restricted area nor survived

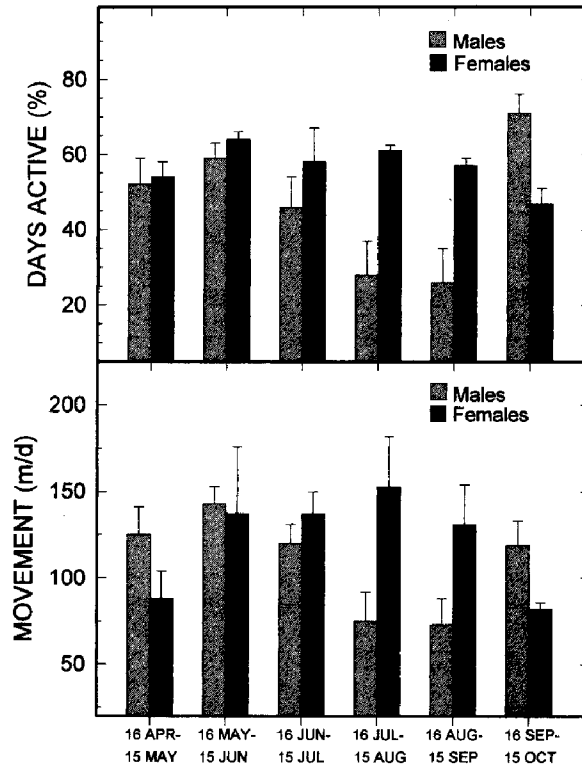


FIG. 2. Frequency of daily activity and movement (pooled for all individuals; excluding days of no movement) by time and sex in eight resident *Heterodon platirhinos* during the activity season (15 April–15 October). Plotted are mean \pm 1 SE.

long enough to warrant calculating home ranges (Tables 1, 2). Although frequency of daily movement (47–57%) and amount of daily movement (~120 m/d) were similar for both resident and translocated snakes (Table 2), variability in amount of daily movement of nonresidents (CV = 58%) was almost six times greater than that of residents (CV = 10%; $F_{8,8} = 65.2$; $P < 0.001$; Zar, 1996). The distributions of daily movements between the groups were similar for movements up to about 400 m, but beyond 400 m, movements were primarily those of translocated snakes. Furthermore, no daily movements >750

TABLE 2. Home range area, frequency of daily movement, amount of daily movement (excluding days of no movement), and variation of daily movement of eight resident and eight translocated *Heterodon platirhinos*. Sample sizes include separate annual estimates for three resident and one translocated snake each of which was tracked over two years. No translocated snake survived long enough in the activity season to warrant calculating a home range.

	Resident N = 11	Translocated N = 9	P
Home range area (ha)	50.2 ± 6.4	—	—
Freq. daily movement (%)	57 ± 4	47 ± 8	$P > 0.05$
Daily movement (m/d)	119 ± 4	120 ± 23	$P > 0.05$
CV daily movement (%)	10	58	$P < 0.001$

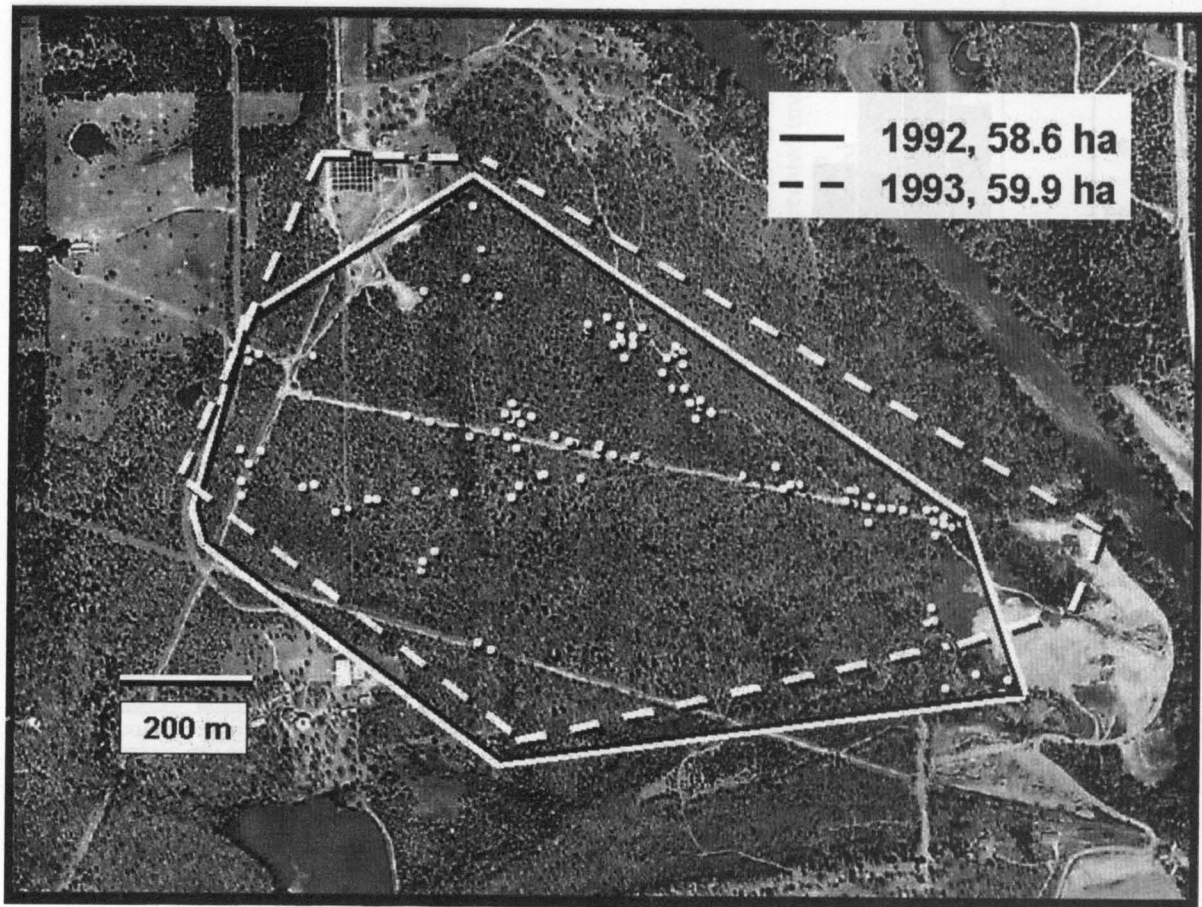


FIG. 3. A typical minimum convex polygon annual home range of a resident *Heterodon platirhinos* (female, no. 1) in successive years. Symbols represent active-day locations for 1992 only (96 of 179 total daily locations).

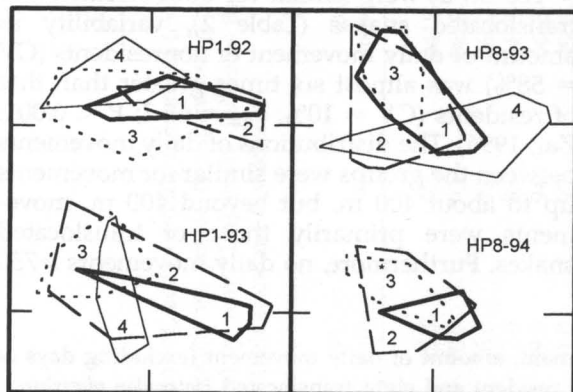


FIG. 4. Time series analysis of annual home ranges of resident *Heterodon platirhinos* in successive years. Plotted are successive 20 active-day locations for two snakes over two years. Successive home ranges are indicated by a (1) thick solid line, (2) dashed line, (3) dotted line, and (4) thin solid line. On 25 August 1994, no. 8 was eaten by an avian predator (at location indicated by asterisk), thus home range for period 4 could not be calculated as it was in 1993. Home ranges are to scale and aligned in two-dimensional space as indicated by tick marks.

m were made by residents, whereas about 4% of daily movements made by translocated snakes exceeded 750 m (Fig. 7). Of five translocated snakes that survived at least 40 total days (including days of no activity), three eventually moved in a mostly unidirectional pattern away from their respective release site (e.g., Fig. 8).

During the course of the study, six of eight resident snakes (75%) were depredated (Table 1). Survivorship of resident snakes within an activity season averaged 122 ± 21 days (Table 3) and was highly variable (CV = 57%). Of eight translocated snakes, at least four (50%) and possibly six (75%) were depredated, depending on whether missing snakes (N = 2) were removed from the study area by predators or were "missing" because of transmitter failure (Table 1). The period of survivorship of translocated snakes within an activity season averaged 36 ± 7 days, was highly variable (CV = 58%), and was significantly less than that of residents (one-tailed Mann-Whitney, $U = 81.0$; Table 3). One-tailed binomial tests indicated that the Trent-Rongstad survival rates of translocated snakes were also

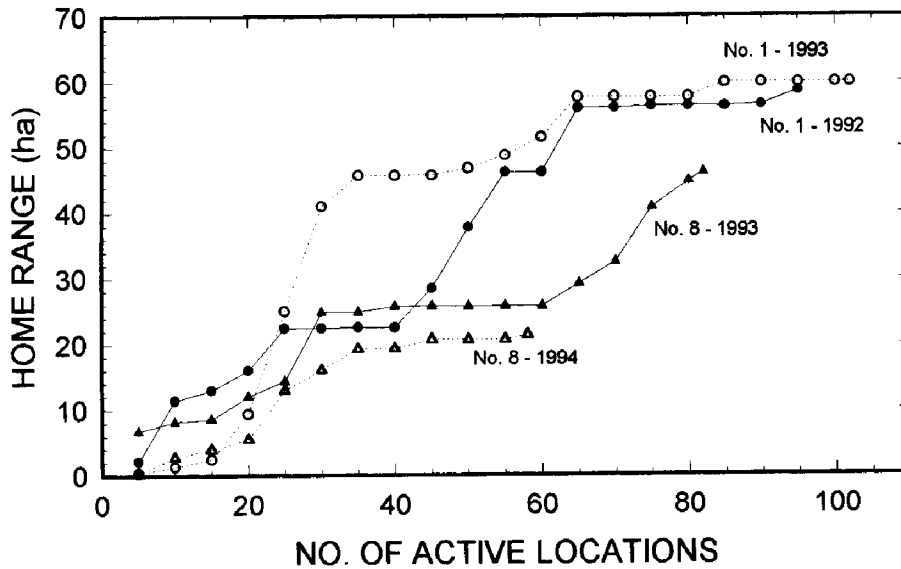


FIG. 5. Home range size of two resident *Heterodon platirhinos* by year as a function of the number of active (excluding days of no movement) locations during the activity season (15 April–15 October). No. 8 was eaten by a predator after 60 locations in 1994.

significantly less than that of resident snakes (Table 3). Total length of survival period from initial capture to the last location, including across years, was significantly less in translocated snakes (63 ± 30 d) than in resident snakes (235 ± 86 d) ($t = 1.86$, $df = 14$, $P < 0.05$).

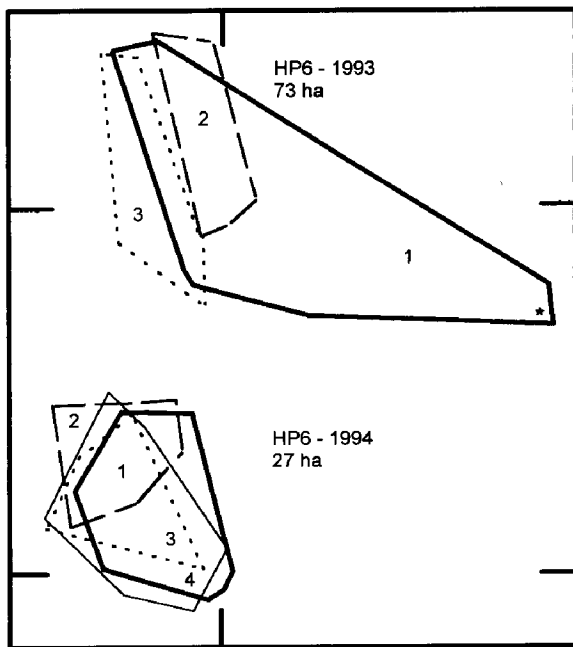


FIG. 6. Time series analysis (successive 20 active-day locations) of the annual home ranges of resident *Heterodon platirhinos* no. 6 in two years. Successive home ranges are indicated as per Fig. 4. Home ranges are to scale and aligned in two-dimensional space as indicated by tick marks. Asterisk indicates overwintering site in the quarry.

DISCUSSION

Preferred habitat of resident *H. platirhinos* in Arkansas was similar to that described for the species in many parts of its range (i.e., dry upland open deciduous/pine forest, forest edge, dry sandy habitats near water; river flood plains; seldom in moist and heavily forested areas; summarized in Platt, 1969). The generally open and dry habitats used by *H. platirhinos* may be related to a preference for maintaining

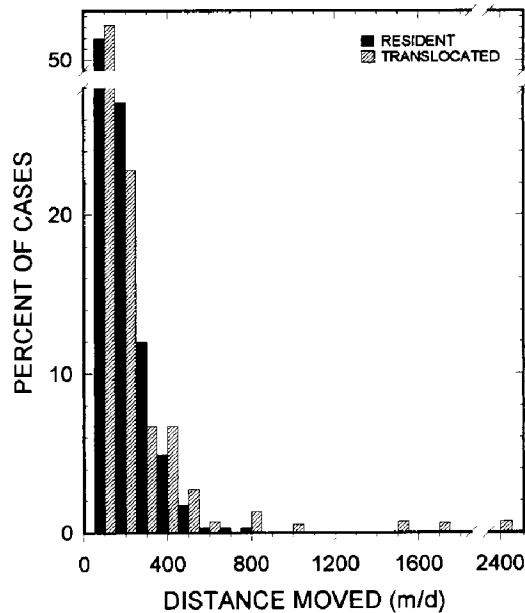


FIG. 7. Frequency of daily movements according to distance moved in resident ($N = 633$ locations) and translocated ($N = 149$ locations) *Heterodon platirhinos* in the activity season (15 April–15 October).

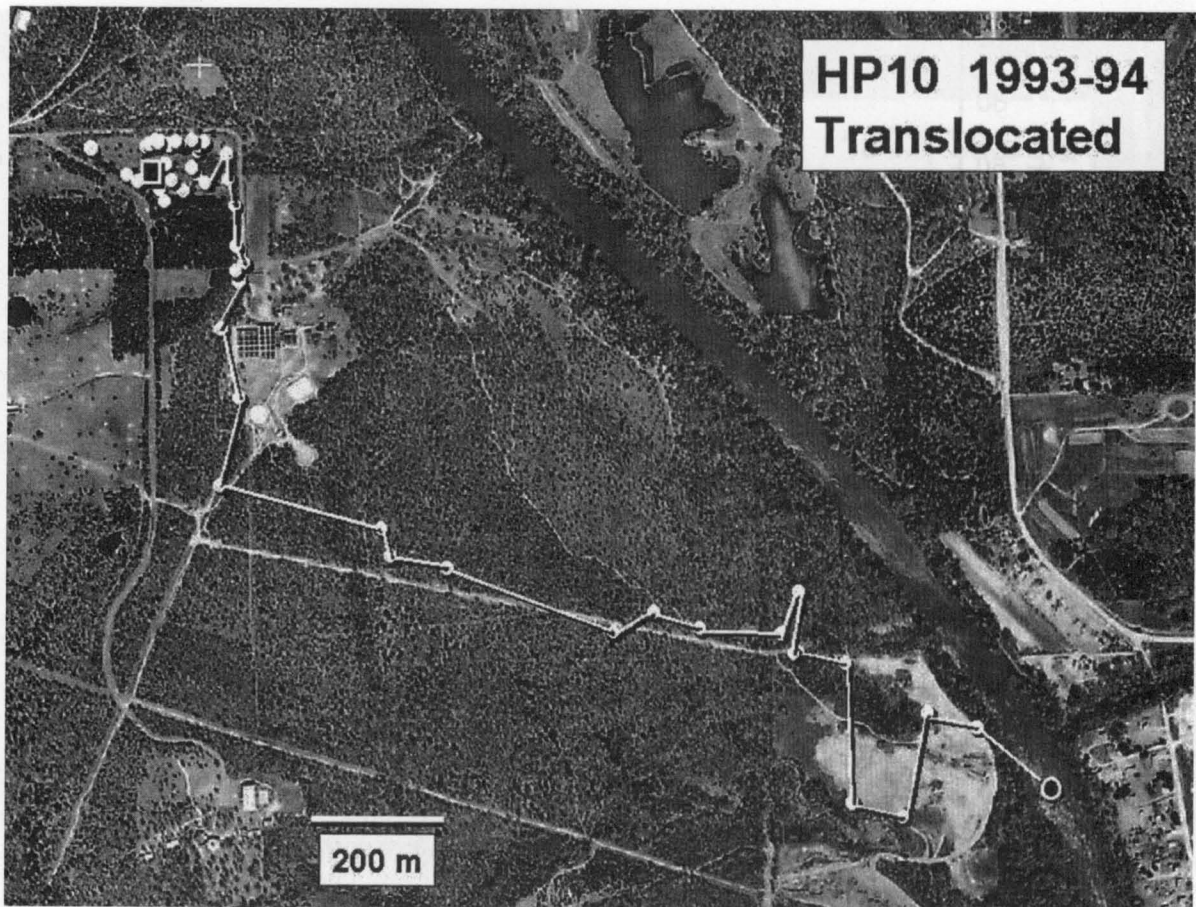


FIG. 8. Movement patterns of *Heterodon platirhinos* no. 10, which survived much longer than any other translocated snake (Table 1). Initially released on 2 July 1993, she quickly moved away from the study area. For 27 days we tracked her off the study area (locations not shown), 16 of which were spent inactive while shedding. After shedding, we again captured, translocated, and released her on the study area at the location indicated by the large dark-centered square on 13 August 1993. She spent the remainder of the 1993 activity and 1993–1994 overwintering seasons within a small area (<2.5 ha) immediately surrounding the release point. After emerging in spring 1994, she left this area and, over a period of about one month, moved unidirectionally to the location indicated by the large dark-centered circle where she was eaten by a fish on 29 April.

relatively high body temperatures (Platt, 1969; Huey, 1991). *Heterodon platirhinos* in Arkansas appeared to be diurnally active as reported by Platt (1969) and Scott (1986) for Kansas and Virginia populations. The frequency of daily activity for individual *Heterodon* (57%) was similar to an average for eight different snake species

(60%; Fitch and Shirer, 1971) and apparently slightly less than values reported for various other telemetered snakes (*Pituophis*, 63%, Grothe, 1992; *Coluber*, 72–80%, Plummer and Congdon, 1994; *Masticophis*, 76%, Secor, 1992; *Sistrurus*, 69%, Johnson, (1995).

In our small sample, males tended to move

TABLE 3. Period of survivorship and Trent-Rongstad survivorship estimates (TR) of eight resident and eight translocated *Heterodon platirhinos* during the annual activity season (15 April–15 October). Trent-Rongstad estimates and their 95% confidence limits were calculated assuming that the three missing snakes with unknown fates either died (TR_m) or were missing due to transmitter failure (TR_{tf}). Data include separate annual estimates for three resident and one translocated snake each of which was tracked over two years.

	Days survive	TR _m survival	TR _{tf} survival
Resident	122 ± 21	0.441 (0.162–0.700)	0.506 (0.199–0.764)
Translocated	36 ± 7	0.015 (0.0002–0.141)	0.043 (0.001–0.257)
Probability	<0.01	<0.01	<0.01

more than females in both spring and fall, a behavior consistent with mate searching behavior (Gibbons and Semlitsch, 1987) for species which mate in both spring and fall as *H. platirhinos* is known to do (Platt, 1969; Plummer and Mills, 1996). Based on the distribution of captures, both Platt (1969) and Gibbons and Semlitsch (1987) found that activity for *H. platirhinos* was seasonally bimodal, with peak periods of activity in the spring and fall. Although based on few individuals, our data suggest that a bimodal seasonal activity pattern may be more characteristic of males than females. A similar mid-summer decrease in male activity has been reported in other snake species (e.g., Feaver, 1977; Madsen, 1984; Plummer, 1985, 1991).

Time series analysis supports the notion that home ranges of individual resident *H. platirhinos* consisted largely of a single, well-defined area. Home ranges of *H. platirhinos* were, except for *Crotalus horridus*, much larger than any of those reported in 45 studies of 33 snake species reviewed by Macartney et al. (1988). More recently, only home ranges of the large boid *Morelia spilota* (males, 52 ha; Slip and Shine, 1988) and the wide-foraging *Masticophis flagellum* (53 ha; Secor, 1992) are reported to be roughly the size of those of *H. platirhinos* (50 ha). Macartney et al. (1988) suggested that species-specific home range and movement patterns may not exist in snakes, and much of the spatial and temporal variation in movements of wide-ranging species (e.g., *Pseudechis porphyriachus*, Shine, 1987; *Coluber constrictor*, Plummer and Congdon, 1994; *Morelia spilota*, Slip and Shine, 1988; Shine and Fitzgerald, 1996) is thought to result primarily from spatial and temporal differences in resources (Gregory et al., 1987; Macartney et al., 1988; Plummer and Congdon, 1994; Shine and Fitzgerald, 1996). Whether the large home ranges for *H. platirhinos* in Arkansas are taxon-specific or result from widely dispersed resources remain to be determined.

If resident snake no. 1, lost to an unknown cause (Table 1), was assumed to have been lost because of transmitter failure and thus in fact survived, the calculated Trent-Rongstad survivorship for resident adults during the activity season was ~50% (Table 3). Assuming that predation during the activity season was the major source of mortality and overwintering mortality was negligible, this value is similar to the 47% annual survivorship calculated from Platt's (1969) mark-recapture data by Parker and Plummer (1987), and is in accordance with the life history of *H. platirhinos* which is characterized by relatively early maturation, high fecundity, and high mortality (Platt, 1969; Parker and Plummer, 1987).

Resident and translocated hognose snakes ap-

peared to behave similarly in terms of frequency and amount of daily movement, and the few body mass data suggest that translocated snakes were able to forage successfully. Similar results in behavior between resident and translocated snakes have been reported in *Morelia spilota* (Shine and Fitzgerald, 1996) and *Crotalus horridus* (Reinert and Rupert, 1999). However, as in *C. horridus* (Reinert and Rupert, 1999), our data demonstrated that translocated hognose snakes did not survive as long as resident snakes and exhibited aberrant movement patterns in terms of confinement to a specific area. Home range theory suggests a possible causal link between aberrant movements and decreased survivorship. Home range theory is predicated on familiarity with habitat (Brown and Orians, 1970), and our data show that individual resident *H. platirhinos* normally move in ways that strongly suggest familiarity with and confinement to a specific home range area. Furthermore, moving snakes likely are at greater risk of predation than when inactive (e.g., Andren, 1985; Madsen and Shine, 1993; Shine and Fitzgerald, 1996). Motivated by exploration and/or search for familiar landmarks, unfamiliarity with habitat could result in snakes making extended undirected movements in high risk areas (e.g., high visibility to predators). From a conservation perspective, these results suggest that using adult translocation to augment declining populations in another area may not be an effective strategy for some snakes, particularly for highly mobile but inoffensive species such as *H. platirhinos*. However, the paucity of translocation studies in snakes precludes broad conclusions at this time. For example, movement patterns and perhaps survivorship may be less affected by translocation for more sedentary snake species provided that such snakes are released into optimal habitats (Shine and Fitzgerald, 1996; Shine, pers. comm.).

Acknowledgments.—We thank M. May for assistance in the field, J. Hollaway and S. Henson for permitting us access to properties under their charge, J. Moon for providing logistical support, and H. Reinert for providing an unpublished manuscript. W. Arnold, J. Demuth, M. Gregory, J. Pryor, and C. Shadrix provided offsite *Heterodon* for translocation. Collection of snakes was authorized by Scientific Collection Permits issued by the Arkansas State Game and Fish Commission. Treatment of snakes was approved by the Harding University Animal Care Committee. For insightful discussions on snake movements and/or comments on the manuscript, we thank J. Demuth, H. Greene, S. Plummer, and H. Reinert. We are greatly indebted to two anonymous reviewers for their yeoman's work. This study was partially supported by several faculty development grants from Harding University.

LITERATURE CITED

- ANDREN, C. 1985. Risk of predation in male and female adders, *Vipera berus* (Linne). *Amphibia-Reptilia* 6:203-206.
- BOYER, D. A., AND R. D. BROWN. 1988. A survey of translocations of mammals in the United States 1985. In L. Nielsen and R. D. Brown (eds.), *Translocations of Wild Animals*, pp. 1-11. Wisconsin Humane Society, Milwaukee, Wisconsin.
- BROWN, J. L., AND G. H. ORIANS. 1970. Spacing patterns in mobile animals. *Ann. Rev. Ecol. Syst.* 1: 239-262.
- DODD, C. K., JR. 1987. Status, conservation, and management. In R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), *Snakes, Ecology and Evolutionary Biology*, pp. 478-513. Macmillan Publ. Co. New York.
- . 1993. Strategies for snake conservation. In R. A. Seigel and J. T. Collins (eds.), *Snakes, Ecology and Behavior*, pp. 363-393. McGraw-Hill, Inc. New York.
- , AND R. A. SEIGEL. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? *Herpetologica* 47:336-350.
- DURNER, G. M., AND J. E. GATES. 1993. Spatial and activity patterns and movements of black rat snakes on Remington Farms, Maryland. *J. Wildl. Manag.* 57:812-826.
- FEAVER, P. E. 1977. The demography of a Michigan population of *Natrix sipedon* with discussions of ophidian growth and reproduction. Unpubl. Ph.D. Diss., Univ. Michigan, Ann Arbor.
- FITCH, H. S., AND H. S. SHIRER. 1971. A radiotelemetric study of spatial relationships in some common snakes. *Copeia* 1971:118-128.
- FOTI, T. L. 1974. Natural divisions of Arkansas. In Arkansas Department of Planning (ed.), *Arkansas Natural Area Plan*, pp. 11-34. Little Rock.
- , X. LI, M. BLANEY, AND K. G. SMITH. 1994. A classification system for the natural vegetation of Arkansas. *Proc. Arkansas Acad. Sci.* 48:50-62.
- GALLIGAN, J. H., AND W. R. DUNSON. 1979. Biology and status of timber rattlesnake (*Crotalus horridus*) populations in Pennsylvania. *Biol. Conserv.* 15:13-58.
- GIBBONS, J. W., AND R. D. SEMLITSCH. 1987. Activity patterns. In R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 396-421. MacMillan, New York.
- GREGORY, P. T., J. M. MACARTNEY, AND K. W. LARSEN. 1987. Spatial patterns and movements. In R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 366-395. MacMillan, New York.
- GRIFFITH, B., J. M. SCOTT, J. W. CARPENTER, AND C. REED. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245:477-480.
- GROTHER, S. 1992. Red-tailed hawk predation on snakes: the effects of weather and snake activity. Unpubl. M.S. Thesis, Idaho State Univ., Pocatello.
- HUEY, R. B. 1991. Physiological consequences of habitat selection. *Amer. Natur.* 137:S91-S115.
- JOHNSON, G. 1995. Spatial ecology, habitat preference, and habitat management of the Eastern massasauga, *Sistrurus c. catenatus* in a New York weakly-minerotrophic peatland. Unpubl. Ph.D. Diss. State Univ. New York, Syracuse.
- KREBS, C. J. 1989. *Ecological Methodology*. Harper & Row Publ., New York.
- LANDRETH, H. F. 1973. Orientation and behavior of the rattlesnake, *Crotalus atrox*. *Copeia* 1973:26-31.
- MACARTNEY, J. M., P. T. GREGORY, AND K. W. LARSEN. 1988. A tabular survey of data on movements and home ranges of snakes. *J. Herpetol.* 22:61-73.
- MADSEN, T. 1984. Movements, home range size and habitat use of radio-tracked grass snakes (*Natrix natrix*) in southern Sweden. *Copeia* 1984:707-713.
- , AND R. SHINE. 1993. Costs of reproduction in a population of European adders. *Oecologia* 94: 488-495.
- PARKER, W. S., AND M. V. PLUMMER. 1987. Population ecology. In R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 253-301. Macmillan Publ. Co. New York.
- PLATT, D. R. 1969. Natural history of the hognose snakes, *Heterodon platyrhinos* and *Heterodon nasicus*. Univ. Kansas Publ. Mus. Nat. Hist. 18:253-420.
- PLUMMER, M. V. 1985. Demography of green snakes (*Opheodrys aestivus*). *Herpetologica* 41:373-381.
- . 1990. Nesting movements, nesting behavior, and nest sites of green snakes (*Opheodrys aestivus*) revealed by radiotelemetry. *Herpetologica* 46:186-191.
- . 1991. Habitat utilization, diet and movements of a temperate arboreal snake (*Opheodrys aestivus*). *J. Herpetol.* 15:425-432.
- , AND J. D. CONGDON. 1994. Radiotelemetric study of activity and movements of racers (*Coluber constrictor*) associated with a Carolina bay in South Carolina. *Copeia* 1994:20-26.
- , AND N. E. MILLS. 1996. Observations on trailing and mating behaviors in hognose snakes (*Heterodon platyrhinos*). *J. Herpetol.* 30:80-82.
- REINERT, H. K. 1991. Translocation as a conservation strategy for amphibians and reptiles: some comments, concerns, and observations. *Herpetologica* 47:357-363.
- . 1992. Radiotelemetric field studies of pitvipers: data acquisition and analysis. In J. A. Campbell and E. D. Brodie, Jr. (eds.), *Biology of the Pitvipers*, pp. 185-197. Selva, Tyler, Texas.
- . 1993. Habitat selection. In R. A. Seigel and J. T. Collins (eds.), *Snakes: Ecology and Behavior*, pp. 201-240. McGraw-Hill, Inc. New York.
- , AND R. R. RUPERT, JR. 1999. Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridus*. *J. Herpetol.* 33:45-61.
- SCOTT, D. 1986. Notes on the eastern hognose snake, *Heterodon platyrhinos* Latreille (Squamata: Colubridae), on a Virginia barrier island. *Brimleyana* 12: 51-55.
- SCOTT, N. J., JR., AND R. A. SEIGEL. 1992. The management of amphibians and reptile populations: species priorities and methodological and theoretical constraints. In D. R. McCullough and R. H. Barrett (eds.), *Wildlife 2001: Populations*, pp. 343-368. Elsevier Applied Sci., London.
- SECOR, S. M. 1992. Activities and energetics of a sit-and-wait foraging snake, *Crotalus cerastes*. Unpubl. Ph.D. Diss., Univ. California, Los Angeles.
- . 1994. Ecological significance of movements

- and activity range for the sidewinder, *Crotalus cerastes*. *Copeia* 1994:631–645.
- , AND K. A. NAGY. 1994. Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology* 75:1600–1614.
- SHINE, R. 1987. Intraspecific variation in thermoregulation, movements and habitat use by Australian blacksnakes, *Pseudechis porphyriachus* (Elapidae). *J. Herpetol.* 21:165–177.
- , AND M. FITZGERALD. 1996. Large snakes in a mosaic rural landscape: the ecology of carpet pythons *Morelia spilota* (Serpentes: Pythonidae) in coastal eastern Australia. *Biol. Conserv.* 76:113–122.
- SLIP, D. J., AND R. SHINE. 1988. Habitat use, movements and activity patterns of free-ranging diamond pythons, *Morelia spilota spilota* (Serpentes: Boidae): a radiotelemetric study. *Aust. Wildl. Res.* 15:515–531.
- SYSTAT, INC. 1992. SYSTAT for Windows: Statistics, Ver. 5. Evanston, Illinois.
- WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, Inc. New York.
- WILSON, A. C., AND M. R. STANLEY PRICE. 1994. Reintroduction as a reason for captive breeding. In P. J. S. Olney, G. M. Mace, and A. T. C. Feistner (eds.). *Creative Conservation: Interactive Management of Wild and Captive Animals*, pp. 243–264. Chapman & Hall, New York.
- ZAR, J. H. 1996. *Biostatistical Analysis*. Prentice-Hall, Inc. Upper Saddle River, New Jersey.

Accepted: 21 July 2000.