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HOME RANGES, MOVEMENT, AND DEN USE IN LONG-BEAKED ECHIDNAS, *ZAGLOSSUS BARTONI*, FROM PAPUA NEW GUINEA

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Long-beaked echidnas (*Zaglossus*), which are endemic to New Guinea, are the largest and least-studied of the 3 extant genera of monotremes. *Zaglossus* is listed as endangered by the World Conservation Union and data regarding the natural history of long-beaked echidnas are critical to efforts to protect these animals. However, no detailed studies of the ecology of this genus have been published. From 2000 to 2005, I captured 22 *Zaglossus bartoni* in the Crater Mountain Wildlife Management Area in Simbu Province, Papua New Guinea. Mean body masses for these animals were 6.5 kg ± 1.4 *SD* ($n = 15$, range: 4.2–9.1 kg) for adults and 4.3 ± 7.4 kg ($n = 6$, range: 3.2–5.1 kg) for juveniles. Eleven of the adults captured were followed via radiotelemetry for 1–12 months. The home ranges for these individuals varied in size from 10 to 168 ha. Home-range size was not correlated with body mass, age, or sex. Long-beaked echidna dens were most commonly located in underground burrows, although individual echidnas favored different types of den sites. Mean burrow length was 2.7 m ± 1.8 *SD* ($n = 5$, range: 1.3–4.9 m) and mean den depth was 0.48 m ± 7.8 *SD* ($n = 5$, range: 0.42–0.57 m) below the soil surface. Animals were never found foraging in daylight. Although no animals were found with eggs or young in the pouch, 1 individual was lactating when captured in April 2002 and again in April 2005. The data generated by this study provide valuable insights into echidna biology that will facilitate efforts to conserve populations of these unusual mammals.

Key words: home range, long-beaked echidna, monotreme, Papua New Guinea, *Zaglossus*

The only extant monotremes, or egg-laying mammals, are the platypus (*Ornithorhynchus anatinus*) and the echidnas. Two distinct genera of echidnas are recognized—short-beaked echidnas (genus *Tachyglossus*, containing a single species) and long-beaked echidnas (genus *Zaglossus*, containing 3 species). Short-beaked echidnas occur throughout the Australian continent, on Tasmania and Kangaroo Island (Griffiths and Simpson 1966; Rismiller 1999), and in New Guinea. Currently, long-beaked echidnas occur only in New Guinea and on immediately adjacent satellite islands, although an extinct species of *Zaglossus* occurred in Australia until the late Pleistocene (Flannery 1995; Long et al. 2002). In New Guinea, *Zaglossus* was historically widespread, spanning the full east–west length of the island and occurring at elevations ranging from sea level to at least 4,150 m, although the animals were absent from the Trans-Fly plains and much of lowland northern New Guinea (Flannery 1995).

Until recently, all long-beaked echidnas were classified as a single species, *Z. bruijni* (see Van Deusen and George 1969). However, Flannery and Groves (1998) recognized 3 species of *Zaglossus* based on variation in skull morphology, body size, pelage characteristics, and the number of clawed toes on the fore and hind feet. The western long-beaked echidna (*Z. bruijni* Peters and Doria 1876) is endemic to the Vogelkop region of western New Guinea, including the Arfak, Tamrau, Fak Fak, and (possibly) Charles Louis Mountain ranges as well as the island of Salawati. In contrast, the eastern long-beaked echidna (*Z. bartoni* Thomas 1907) is found in the Central Cordillera and in Huon Peninsula. Finally, the cyclops long-beaked echidna (*Z. attenboroughi* Flannery and Groves 1998), the smallest of the long-beaked echidnas, is known only from near Jayapura in the Cyclops Mountains in western New Guinea.

Apart from several recent accounts of taxonomy, morphology, and geographic distribution (e.g., Flannery and Groves 1998; Menzies 1991; Musser 2003), information about the biology of free-living long-beaked echidnas is largely

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nonexistent. Several factors appear to have contributed to this shortcoming. Long-beaked echidnas are nocturnal, elusive, and forage primarily in areas where there is little human disturbance, making them extremely difficult to find in the wild (Flannery 1995; Flannery and Groves 1998; Helgen 2007a). In addition, the arrangement of their spines differs from that found on short-beaked echidnas, making it difficult to use the same methods of attaching radiotransmitters that have allowed successful studies of *Tachyglossus* (Rismiller 1999). Collectively, these attributes have hampered efforts to study long-beaked echidnas in the wild.

Our limited knowledge of the biology of long-beaked echidnas means that little information is available to aid the development of guidelines for echidna conservation in New Guinea. The principal threats to long-beaked echidnas are loss of habitat and hunting pressure (Flannery and Groves 1998), both of which are prevalent in the areas of New Guinea where *Zaglossus* occurs. The primary objective of this study was to develop methods for studying long-beaked echidnas in the wild. These procedures were used to radiotrack individuals, to estimate home-range sizes, and to characterize patterns of movement and den use. Examination of the resulting data yields important new insights into long-beaked echidna biology that should facilitate efforts to protect these unusual animals.

Materials and Methods

Study area.—This study was conducted at 3 sites in Crater Mountain Wildlife Management Area in southern Simbu Province, Papua New Guinea. Preliminary data were collected during 4 periods: March–November 2001, March–July 2002, September–October 2002, and April–July 2003. Intensive radiotracking was conducted from November 2004 to December 2005. The main study site at Supa (06°40′09″S, 145°03′27″E) covered approximately 20 km^2. I also studied long-beaked echidnas at Seino (06°41′06″S, 145°03′39″E) and at Aedo (06°40′51″S, 145°06′41″E). The vegetation at Supa was open heterogeneous forest with relatively sparse vegetation made up of scattered scrambling bamboos (*Nastus*), palms, and climbing rattans, with the ground surface partially covered with mosses. In contrast, the vegetation at Seino and Aedo was dominated by *Lithocarpus megacarpus* (Fagaceae) and *Agathis* (Araucariaceae) and trees were typically of small stature and had conspicuous buttresses covered with moss. The climate in the Crater Mountain Wildlife Management Area was humid; rainfall, which occurred throughout the year, averaged 6.4 m annually. Daily temperatures ranged from 15°C to 28°C (Wright et al. 1997).

Foraging signs and capture of study animals.—Long-beaked echidnas retrieve earthworms by digging them out of the forest soil using the combined effort of the forelimbs and the snout (Menzies 1991). As a result, they leave depressions in the soil similar to those of the short-beaked echidna; I refer to these depressions as digs or feeding signs. Fresh digs or feeding signs from the previous night's foraging could be distinguished from those made during preceding nights (older digs) because the latter were often covered with loose soil and leaves; following wet nights, older digs also were filled with water.

Because short-beaked and long-beaked echidnas co-occur at Supa, it was important to distinguish between the feeding signs of each species. "Nose pokes" of short-beaked echidnas are never deeper than approximately 5 cm (P. D. Rismiller, University of Adelaide, pers. comm.) and, hence, all nose pokes and digs deeper than 5 cm were presumed to be made by long-beaked echidnas. During the day, I and my assistants looked for signs of recent feeding such as nose pokes made when the animals inserted their beaks into the soil while foraging. When evidence of recent foraging by a long-beaked echidna was found, we followed the trail of nose pokes to the animal's den site, where the echidna could be captured by digging it out of its burrow. At night, we returned to the den sites located during the preceding day and used spotlights to search around fresh digs until the animal was located. In 2004, searches were conducted only on mornings following nights during which rain stopped before daybreak. This maximized our search efforts, because the moist soil made it easy to locate foraging digs and to follow fresh tracks to dens. Underground dens were excavated and hollow logs were cut open to capture echidnas. All methods used in this study met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Study animal measurement and identification.—Captured echidnas were placed in cloth bags and carried approximately 500 m to 2 km to my campsite, where body mass, head–body length, and snout (i.e., "beak") length were recorded. I also recorded number of toes on each foot to compare the study population with western long-beaked echidnas (*Z. bruijni*), which have 4 toes. Hair samples, ectoparasites (Beati et al. 2008), and feces were collected from all individuals and preserved in 90% ethanol. The age of each echidna (juvenile versus adult) was determined based on the condition of the spurs on the hind feet; juveniles have a sheath covering the spur, whereas the sheath is absent in adults (Rismiller 1999). Because all juvenile long-beaked echidnas have a spur (Griffiths 1978; M. Opiang, pers. obs.) and retention of the spur into adulthood can vary (see below), I did not use the presence of the spur to determine the sex (cf. Flannery and Groves 1998; Van Deusen and George 1969). Instead, I palpated the pouch at the base of the cloaca to determine the nature of the genitalia and thus establish the sex of an animal (Rismiller and McKelvey 1996, 2000). Reproductive condition was assessed by looking for a protruding penis (an indication of sexual activity) or lactating nipples (a sign of breeding). A microchip passive integrated transponder tag with a unique code (Biomark, Inc., www.biomark.com) was inserted under the skin at the right shoulder of each captured echidna for long-term identification. For visual identification, distinctive color combinations of heat-shrink tubing were placed over the spines in 4 areas (right and left shoulder, and right and left rump) to provide each animal with a unique mark.

Transmitter attachment.—Several methods were used to attach radiotransmitters to both adult and juvenile study animals. During 2001, transmitters (weight: 90 g; Titley Electronic, Pty., Ltd., Ballina, New South Wales, Australia) were attached to the backs of 5 echidnas by tying the transmitters to a plastic mesh that had been glued to the animal with epoxy resin. The mesh and transmitter were attached to the animal's dorsum, just anterior to the base of the tail. To facilitate adherence of the mesh to the animal, the spines and fur in this region were clipped to a length of less than 1 cm. During 2002, transmitters (weight: 50 g; Biotelemetry Tracking, St. Agnes, South Australia, Australia) were attached to 2 animals using the same method as above, but without the plastic mesh. In addition, a transmitter (weight: 6 g; Holohil, Ltd., Carp, Ontario, Canada) was attached to 1 animal by tying it to a set of spines on the mid-lower back that had been treated with epoxy resin so that the transmitter package sat on top of the spines, rather than directly on the echidna's back. Finally, in 2003, a transmitter (weight: 6 g; Holohil, Ltd.) was attached to an echidna's ankle. Specifically, the transmitter was sewn onto nylon webbing and the webbing was then sewn around the ankle, just above the spur, with the transmitter on the outer surface of the leg and the transmitter antenna pointing upward. This method appeared to be the most reliable and was used to attach transmitters to 9 animals during 2004 and 2005. In these final 2 years of the study, however, a more durable spider-wire was used to stitch the transmitter to the webbing and to secure the webbing around the ankle. All transmitters had 30-cm whip antennas, emitted signals between 150 and 152 MHz, and had a battery life span of 6 months.

Radiotracking.—Animals with transmitters, both adults and juveniles, were located using very-high-frequency receivers (Telonics, Inc., Mesa, Arizona) and directional antennae (TR-2 elements: Telonics, Inc.; and TR-3 elements: Titley, Ltd.). From open hilltops, transmitter signals could typically be detected over distances of approximately 1 km. This distance decreased to <100 m in gullies and heavily wooded areas and to <20 m when echidnas were using dens located in limestone holes. At night I tried to estimate the study animals' location by triangulation or by locating them while they were foraging. However, this proved to be difficult because of the ruggedness of the terrain and because echidnas were continuously moving as I got closer. Thus, each day I tracked the study animals to their den sites while they were resting and used the locations of daytime den sites to estimate home-range size (see "Home-range analyses" below).

An echidna was determined to be in its den when the radiosignal was strong when I placed the antennae inside the den. I then recorded the type of den (see below), the number of den entrances, the diameters of all entrances, and the slope of the substrate on which the den was located. The location of each den was recorded with a Garmin 12 XL global positioning system unit (Garmin, Inc., Olathe, Kansas). The density of vegetation around the den was estimated visually. A score of 0 was given to those dens whose entrances could clearly be seen from a distance of at least 5 m, a score of 1 was given to dens whose entrances were partially visually obscured by vegetation, and a score of 2 was given to dens whose entrances were completely obscured by vegetation. Den types were categorized as 1 of the following: in plain ground, at the base of a standing tree, in a hollow log, under a log, in a stone crevice, or under surface debris. As the study progressed, echidnas were sometimes found to stay in the same den for more than 1 day. To determine whether an animal was in the den continuously during this period or was instead repeatedly leaving and then reentering the den, a row of small sticks was placed across the entrance or entrances to the den. The animal was determined to have remained in the den continuously if the sticks remained undisturbed.

Home-range analyses.—Each echidna was radiotracked daily for as long as the transmitter stayed on the animal, which ranged from 3 days to 12 months. I used capture locations, the locations of all dens occupied by echidnas during the tracking period, and the sites where detached transmitters were recovered to determine home ranges, because these were the only reliable location data collected during the study. Home ranges were determined using the Animal Movement Extension (www.spatialecology.com/htools) for the Spatial Analyses module of ArcGIS 9.1 (ESRI, Redlands, California). Home-range size was estimated from the 100% minimum convex polygon for each animal. An area observation curve using 100 bootstrap replicates for each sample size indicated that about 25 locations (fixes) were necessary to estimate home-range size using the minimum convex polygon model (Schooley and Branch 2005). Sample sizes for some individuals were smaller than this value; because of the paucity of home-range data for *Z. bartoni*, however, fixes for these animals were analyzed as described above.

Statistical analyses.—Student's *t*-tests were used to examine differences in body mass and snout length between males and females; these were the 1st analyses of sexual dimorphism in *Zaglossus* to be conducted using animals for which sex had been definitively determined (Flannery and Groves 1998). I used 2-sample *t*-tests and Wilcoxon rank sum tests to examine differences in snout length between males and females, and I used Spearmen's rank correlations to explore relationships between body mass and home-range size. A chi-square test was used to determine if echidna den sites were found more in high, medium, or low vegetation density areas. A *G*-test was used to determine if dens were more frequently located above-versus belowground. A Fisher's exact test was used to determine if den locations (above-versus belowground) varied between adults and juveniles. Data from 70 dens identified between 2002 and 2003 were analyzed; all but 1 of the animals occupying these dens were adults. Animals for which sex or age could not be clearly determined were excluded from these analyses. All tests were performed according to Sokal and Rohlf (1969) using Statistix 8 (Analytical Software, Inc., Tallahassee, Florida). Throughout the text, means are reported ±1 *SD*.

Results

Foraging signs.—The average depth of long-beaked echidna digs was 14.8 ± 1.8 cm (range: 12.0–17.5 cm, $n = 26$), with an average width of 6.6 ± 2.1 cm (range: 4.1–13.2 cm, $n = 26$) at the top of the dig. Four different types of digs were recognized (Fig. 1): nose poke—the snout is poked into the soil, but not far enough for the head to leave an impression; head dig—the

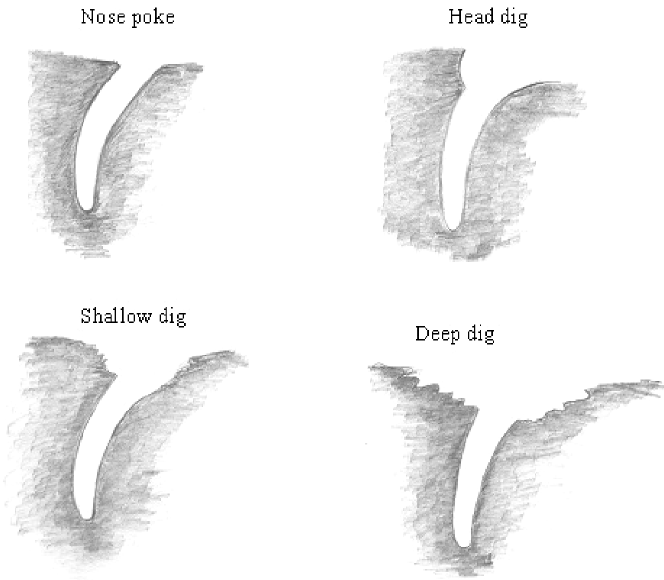

Fig. 1.—Types of digs made by long-beaked echidnas in Crater Mountain Wildlife Management Area. The digs are created through the combined efforts of the forelimbs and the snout, leaving behind a depression resembling the snout. Drawings are based on that author's observations and are not to scale.

snout is poked into the soil far enough that the head leaves a smooth, concave impression in the soil; shallow dig—the head is pushed hard against the soil, disrupting the soil surface and creating a pit that is <8 cm wide; and deep dig—the head is pushed hard against the soil, creating a pit that is >13 cm wide. Long-beaked echidna digs were usually located 50–200 m from an active den. In addition to digs, several logs were found with claw marks that had probably been made by long-beaked echidnas, suggesting that the animals may also forage on wood-boring invertebrates (e.g., grubs).

Animals captured.—Twelve *Z. bartoni* were captured during 2000–2003; 5 of these animals were captured twice. These captures represented 5,899 person-hours of searching for echidna sign. The improved search technique used in 2004 (searching for sign of echidnas after rain) led to an increased rate of capture, with 6 animals caught in 3 weeks (approximately 315 h); this represents 80% of the total sample of 10 animals captured in 2004–2005. In total, 22 long-beaked echidnas, 15 adults and 7 juveniles, were captured between 2001 and 2005. I determined the sexes of 11 adults (3 males and 8 females); the sexes of juveniles could not be reliably determined. There was a significant difference in body mass between adult males and females ($t = 4.68$, $d.f. = 9$, $P = 0.0012$), with females being heavier than males (Table 1). Females had significantly longer snouts than males (Table 1; $t = 2.87$, $d.f. = 9$, $P = 0.018$, Wilcoxon rank sum test, $t = 2.148$, $P = 0.012$) and there was a significant difference in head and body length, with females being longer than males ($t = 2.75$, $d.f. = 9$, $P = 0.022$, Wilcoxon rank sum test, $t = 2.046$, $P = 0.0182$). All long-beaked echidnas captured in Crater Mountain Wildlife Management Area had 5 claws on their fore and hind feet, which is the usual number for *Z. bartoni* (Flannery and Groves 1998). Three adult echidnas (2 males and 1 animal of undetermined sex) weighed less than 3 of the juveniles captured. Therefore, there was no distinct cutoff between the body masses of adults and juveniles.

A lactating long-beaked echidna was captured on 13 April 2002; this animal was still lactating when recaptured on 13 May 2002. The same female was again found to be lactating on 28 April 2005. Presumably, this female had a burrow with young in both 2002 and 2005, although I failed to find it. No long-beaked echidna was found with eggs or young in the pouch, and no male was found with a protruding penis, which would indicate breeding condition.

Success of transmitter attachment.—Transmitters stayed on echidnas for 1 day to 12 months. Transmitters attached to the dorsum stayed on for 1–80 days, with a mean of 35 $\pm$ 27 days ($n = 9$). Four of 9 transmitters that were attached to the dorsal surfaces of animals dropped off those individuals but were recovered. Three other transmitters either failed, dropped off in places where they could not be detected, or the animals dispersed to an area where the signal could not be detected. Three of the transmitters that were recovered had spines and fur attached to them, suggesting that loss of the units may have resulted in minor injury to the study subjects. One echidna that was recaptured 4 days after it lost its transmitter had a small wound where the transmitter had been attached; the wound was cleaned and the individual was released. Two other echidnas captured a year after transmitter loss showed no signs of significant weight loss and the spines and fur at the site of attachment had completely regrown. The anklet attachment method was more effective; only 1 of the 6 transmitters attached using this method became detached during the study. In particular, transmitters attached with spider-wire remained on the animals for 5–6 months and were only removed to replace batteries.

Movements and home ranges.—Home-range sizes (Fig. 2; Table 2) were estimated for 9 adults and 3 juveniles. The mean number of data points (fixes) per individual used to estimate distances moved and home-range sizes was 21 $\pm$ 16 points (range = 4–64 points). All but 2 *Z. bartoni* had sample sizes of <25 fixes because of transmitters dislodging, transmitter failure, or antenna breakage, with the latter being most common. Signals were received from <10 m when an animal was inside the den. On many occasions, *Z. bartoni* remained in a burrow for 2–6 days, and thus the number of location points was often less than the number of days in the tracking period.

The mean home-range size was 39 $\pm$ 47 ha (range = 2.2–68 ha). The smallest home-range size calculated was based on 4 fixes and thus may not have been an accurate representation of actual home-range size for that individual. The largest home range belonged to a dispersing juvenile. This individual moved over an area of 60 ha before the end of data collection. There was no significant correlation between home-range size and body mass ($r = 0.32$, $d.f. = 11$, $P > 0.05$). Distances moved by individuals during a single night ranged from 15 to 823 m ($\bar{X} = 216 \pm 147$ m, $n = 52$).

Den characteristics.—A total of 223 long-beaked echidna den sites were detected during this study, 209 (93.7%) of which

Table 1.—Body mass, snout length, and head–body length for male, female, and juvenile *Zaglossus bartoni*. Only data from individuals for which sex could be reliably determined are included; juveniles were identified based on the presence of a spur sheath.

	Male ($n = 3$)			Female ($n = 8$)			Juvenile ($n = 6$)		
	$\bar{X}$	*SD*	Range	$\bar{X}$	*SD*	Range	$\bar{X}$	*SD*	Range
Body mass (g)	4,659	396.9	4,200–6,500	6,990	762.3	4,300–9,000	4,358	738.7	3,750–4,675
Snout length (cm)	10.7	0.7	10.1–11.6	12.6	1.1	10.8–14.2	10.3	0.4	7.2–11.4
Head–body length (cm)	50.8	3.7	48–55	57.4	3.7	51.5–63.7	49.7	3.6	40.6–55

were underground. The other 14 den sites were at a cliff face or under the cover of thick vegetation. Dens were most commonly located in areas of low vegetation density (61%), followed by areas of medium-density (21%) and then high-density (18%) vegetation; this distribution was significantly different than expected given the distribution of high-, medium-, and low-density vegetation on the study sites ($\chi^2 = 29.2$, *d.f.* = 2, $P <$ 0.001). Of 70 dens found in 2002 and 2003, 53 (76%) were underground burrows, indicating that echidnas used underground dens significantly more than aboveground dens ($G =$ 28.8, *d.f.* = 6, $P < 0.001$). However, juveniles were more likely than adults to use aboveground dens (4 of 40 for adults, 13 of 30 for juveniles; Fisher exact test, $P = 0.08$). Entrances were 20 ± 9.7 cm (range = 9–30 cm, $n = 68$) in diameter and the mean slope of the ground in which den sites were located was 30° ± 16.5° (range = 0–80°, $n = 68$). Average burrow length was 2.7 ± 1.8 m (range = 1.3–4.9 m, $n = 5$), and average distance from the ground surface to the part of the den in which the animal rested was 0.48 ± 7.8 m (range = 0.42–0.57 m, $n = 5$). The resting site within a den was often situated above the level of the entrance hole and at the end of the burrow farthest from the entrance hole (Fig. 3). Most echidnas changed dens each night and rarely reused the same site, although exceptions to this pattern were observed. For example, 1 echidna used the same den for 23 consecutive days, eventually emerging from the den at a new entrance approximately 7 m from the original den entrance. Reuse of dens also may occur across longer time periods; in 2004, 1 long-beaked echidna was found reusing 2 dens that it had used in 2002.

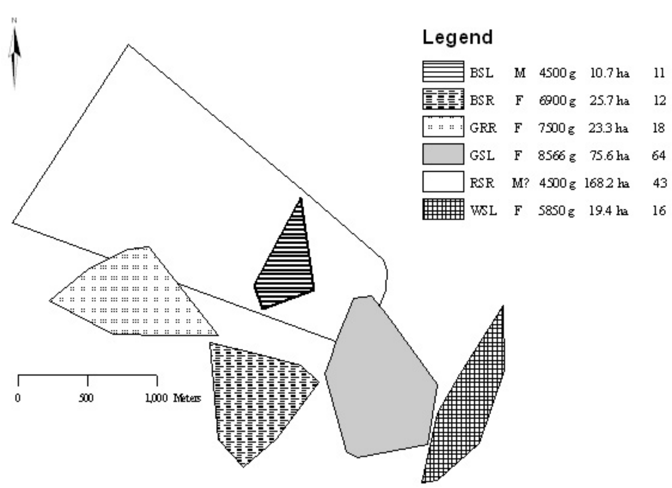

Fig. 2.—Home ranges for 6 *Zaglossus bartoni* radiotracked from January 2004 to January 2005 at Crater Mountain Wildlife Management Area. For each individual, sex, body mass, number of radiofixes, and home-range size are indicated. The largest home range detected belonged to a dispersing juvenile (animal RSR) that eventually settled in an area occupying 60 ha.

Discussion

This study provides valuable new insights into the natural history of long-beaked echidnas, including morphological variation, home-range use, and patterns of den use. Long-beaked echidnas forage mostly at night and feed principally on earthworms, occasionally ripping open logs to locate grubs. Females were generally heavier than males. Dens of long-beaked echidnas were most commonly located in underground burrows, although individual echidnas favored different types of den sites. Home ranges varied considerably in size and did not overlap with each other.

Echidnas are not easily seen or easily trapped. In this study, approximately 500 person-hours were required to encounter the 1st animal. This was similar to 300 person-hours of searching required to encounter short-beaked echidnas on Kangaroo Island in South Australia (Rismiller 1999, 2000). The current study yielded important new insights into methods for locating and capturing long-beaked echidnas, beginning with methods for distinguishing between the foraging signs of long-beaked and short-beaked echidnas, which may forage in the same areas. Digs of long-beaked echidnas were formed more from a "head press" than from digging with the forefeet, and these

Table 2.—Estimates of home-range size for 11 *Zaglossus bartoni* radiotracked during this study. The age, sex, and body mass of each animal are indicated, as are home-range size and the number of telemetry fixes used to assess home ranges. M = male, F = female.

Animal	Age	Sex	Body mass (g)	Home range (ha)	No. fixes
1	Adult	M?	6,500	11.0	14
2	Adult	M	4,500	10.7	11
3	Adult	F	6,900	25.7	12
4	Adult	F	8,566	75.5	64
5	Adult	F	7,500	23.3	18
6	Adult	F	7,975	2.2	4
7	Juvenile	M?	4,350	32.9	14
8	Juvenile	M?	4,500	168.2	43
9	Adult	F	5,850	19.4	16
10	Adult	F	4,600	12.4	21
11	Juvenile	F?	4,300	17.4	15

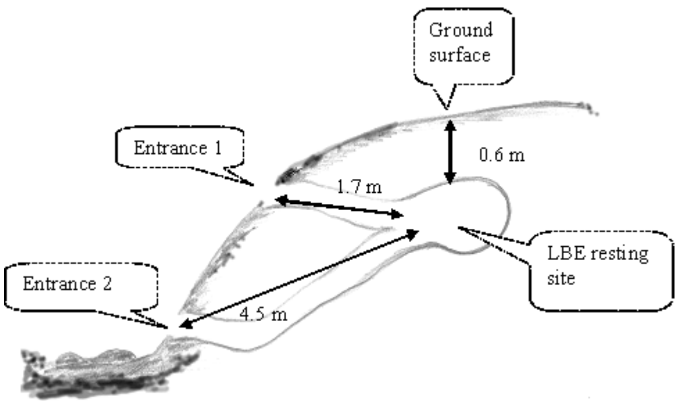

FIG. 3.—Schematic of the typical den structure for *Zaglossus bartoni* at Crater Mountain Wildlife Management Area. Entrances and tunnel lengths are indicated, as is the location of the resting site and its depth below the soil surface.

digs were wider and deeper than those made by short-beaked echidnas. Digs could easily be recognized and followed to dens, particularly if it had rained in the 1st half of the night because then fresh digs could be distinguished from older sites. Once at a potential den site, 2 signs could be used to assess whether the burrow is in use: fresh footprints at the entrance, and the strong smell of echidna scat. This tracking method was only possible in open areas with little ground moss.

The current study also provided valuable insights into methods for monitoring echidna movements and behavior. Long-beaked echidnas do not have a distinct neck and their bodies are covered in hard spines, with the result that conventional transmitter attachment methods (e.g., radiocollars) cannot be used. In addition, transmitters cannot be glued to the midline of the back because the spines of *Zaglossus* are not as heavily rooted as those of short-beaked echidnas and they pull out easily. As demonstrated here, however, transmitters can be attached using anklets. With the anklet method, transmitters remained attached to the study animals for as long as the transmitter battery lasted (5–6 months), with no obvious distress to the animals.

Because I was able to determine the age and sex of many members of the study population, I was able to characterize sexual dimorphism among adult long-beaked echidnas. All juvenile echidnas have a spur and a covering spur sheath (Griffiths 1978; Rismiller 1999). The presence of a spur sheath can be used to age echidnas as either juveniles or adults, at least among females; female echidnas generally lose their spur upon maturity, whereas males retain it (Griffiths 1978). All mature male long-beaked echidnas observed in this study had a spur; 2 mature females also had small spurs, although these had partially shrunk inside the skin. Therefore, the spur is not a reliable indicator of sex. Using more direct examination of the genitalia, however, I was able to confirm that females are larger than males, although, similar to Australian short-beaked echidnas (Rismiller 1999), I found no clear distinction between the body masses of adults and juveniles. Thus, this study also confirmed that body mass alone cannot be used to distinguish between juvenile and adult echidnas.

There was considerable variation in the home-range sizes of long-beaked echidnas in the study population, a pattern also reported for short-beaked echidnas in Australia (Augee et al. 1975, 1992; Wilkinson et al. 1998). I found no clear evidence that the home ranges of adult long-beaked echidnas overlapped, although home ranges of juveniles sometimes overlapped with those of adult females. It seems likely that these juveniles were the offspring of the adult in question and had not yet established their own home ranges. Sample sizes for some animals were small and thus additional telemetry studies of the population are needed. Nevertheless, the results reported here provide valuable preliminary data regarding home-range sizes and patterns of space use by long-beaked echidnas.

Dens of long-beaked echidnas tended to be located belowground in areas of low vegetation density. Most dens were found on slopes, perhaps because slopes are easier to dig into and allow the animal to create resting sites that are uphill of the entrance, thereby avoiding flood runoff. Avoiding predation is often cited as a reason for sheltering in a den (Rismiller 1999) and this might explain the overall preference for underground dens. Little is known about nonhuman predators of long-beaked echidnas. Thylacines (*Thylacinus*), now extinct, occurred in the mountains of New Guinea until the Holocene, and feral domestic dogs, introduced several millennia ago, occur in some high mountain areas in New Guinea today (Helgen 2007b); both are likely predators of long-beaked echidnas. Long-beaked echidnas are often found sheltering under leaves, rather than in dens, in the most rugged part of the Crater Mountain Wildlife Management Area where few people visit. Rather than reduced predation pressure, however, this may reflect the greater abundance of echidnas in such areas, which may lead to more competition for burrows. Juvenile echidnas in the Crater Mountain Wildlife Management Area use aboveground dens more often than adults. The former may be inexperienced and unaware of the location of underground dens or they could still be searching for an area to establish a home range. The dispersing juvenile detected in this study initially used aboveground dens but then burrowed underground after settling in its new home range.

Limited information on the life history, ecology, breeding biology, and feeding behavior of long-beaked echidnas in the wild has precluded development of conservation management plans for these animals. Although much remains to be learned about echidnas, this study provides valuable information regarding the natural history of *Z. bartoni*. Using the study methods described here, it will be possible to generate critical data needed to protect and manage long-beaked echidnas throughout their geographic range.

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