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Home Range, Population Density, and Food Resources of *Agouti paca* (Rodentia: Agoutidae) in Costa Rica: A Study Using Alternative Methods[1]

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ABSTRACT

Field studies of elusive mammals such as *Agouti paca* are difficult, and results are often biased and incomplete because the animals are nocturnal and avoid traps. By studying an *A. paca* population in a Pacific lowland forest of Costa Rica, we developed indirect observational methods to estimate population density and food resource utilization. To estimate population density, we divided the number of *A. paca* burrows found in a 12-ha census area by the average number of burrows utilized per individual from radiotelemetry data. We compared this estimate to independent population estimates obtained using two transect methods. *Agouti paca* density was estimated at 93 individuals/km^2 based on burrow number, and between 67 to 70 individuals/km^2 using transect methods. This discrepancy corroborates previous studies suggesting that transect methods underestimate population density. To identify food resources consumed by the species, we collected fruits and seeds with unambiguous *A. paca* teeth marks. The only animal in Central America with an incisor width similar to *A. paca* is *Dasyprocta variegata*; in a comparison of both species, however, we found that *A. paca* had a significantly larger incisor width and that teeth marks of 4 mm or wider unambiguously indicated handling by this species. By applying this technique, food resources utilized by *A. paca* can be identified more easily than by direct observation. At our study site, we identified 33 plant species consumed by *A. paca*; 61 percent are new records for this animal. Our results suggest that *A. paca* plays a major, although not fully understood, ecological role in seed predation and dispersal.

RESÚMEN

Estudios de campo sobre mamíferos elusivos como las *Agouti paca* son intensivos tanto en tiempo como en labor, y resultan frequentemente parcialisados y incompletos debido a que estos animales son nocturnos y le temen a las trampas. Durante un estudio de la población de *A. paca* en un bosque lluvioso de Costa Rica, desarrollamos métodos de observación indirectos para estimar la densidad y uso de recursos de la población. Para estimar la densidad de la población, dividimos el número de madrigueras en el area de doce hectáreas por el número promedio de madrigueras utilizados por un individuo de los resultados de radiotelemetría. Comparamos esto estimado con otros obtenidos independientemente por métodos de transecto. Basado en el número de madrigueras, se estimó la densidad de *A. paca* en 93 animales/km^2, mientras que los estimados basados en observaciones de transectos dio entre 67 a 70 animales/km^2. Tal diferencia podría confirmar estudios previos indicando que los métodos de transecto subestiman la densidad de poblaciones. Con el fin de identificar los recursos alimenticios consumidos por esta especie, recolectamos frutos y semillas marcas dentales de pacas. El único animal en América Central con un ancho de diente incisivo similar al de la *A. paca* es *Dasyprocta variegata*. En una comparación de las dos especies encontramos que las *A. paca* tenían incisivos significativamente más anchos, y que marcas dentales de 4 mm o más indican sin ambigüedad manipulación por esta especie. Aplicando esta técnica, se puede identificar los recursos alimenticios utilizados por *A. paca* más fácilmente que mediante observaciones directas. En nuestro sitio de estudio identificamos 33 especies de plantas consumidas por pacas: 61 porciento son registros nuevos para este animal. Nuestros resultados indican que las *A. paca* representan una parte muy importante, pero todavía no muy bien entendida, en la depredación y dispersión de semillas.

Key words: Agouti paca; *burrow density; Costa Rica; food resources; home range; Neotropics; population density; seed dispersal; tepezcuintle.*

"... Seinem Temperament entsprechend ist das Paka ein mürrischer Griesgram und Philister, den nur Zorn und Sorge aus seinem Stumpfsinn aufzurütteln vermögen. . ." (Göldi 1914)

AGOUTI PACA (RODENTIA: HYSTRICOMORPHA: AGOUTIDAE) IS A SECRETIVE NOCTURNAL ANIMAL of the Neotropics. *Agouti paca* (paca) may reach *ca* 795 mm in length from head to tail and weigh up to 12 kg (Nowak 1991, Perez 1992). Pacas currently

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range from southern Mexico to northern Argentina at altitudes from sea level to 2000 m (Collett 1981; Eisenberg 1989; Nowak 1991; Perez 1983, 1992). In much of the pacas' historical range, they are endangered or locally extinct due to hunting pressure and habitat loss (Leopold 1972, Matamoros 1982, Smythe 1983, Dirzo & Miranda 1991, Perez 1992, Estrada *et al.* 1994). Pacas have been found to occupy home ranges of 2 to 3 ha (Marcus 1984, Smythe *et al.* 1985) and estimated densities range from 3.5 individuals/km^2 in Peru (Emmons 1987) to 93/km^2 in Puente Gloria, Colombia (Collett 1981).

Transect censusing is a common method for estimating population densities of birds and mammals (*e.g.*, Eisenberg & Thorington 1973; Cant 1977; Terborgh 1983; Emmons 1984, 1987; Glanz 1985; Malcolm 1990; Estrada *et al.* 1994; Wright *et al.* 1994; Voss & Emmons 1996). This direct observation method can be difficult, time and labor intensive, and tends to underestimate animal densities (Dasmann & Mossman 1962, Emlen 1971)—in some cases by up to one-half of the actual number of individuals, as in *Proechimys* (Emmons 1984), *Aotus, Agouti,* and *Sciurus* (Glanz 1985). Frequency of paca footprints has been used as an indirect method of estimating density (Eisenberg *et al.* 1979), but successful application of this method depends highly upon the soil type, leaf litter, and season. A simpler alternative method for density estimation is counting the number of conspicuous structures (*e.g.*, burrows) produced by resident animals (Conroy 1996). For species in which the average number of burrows used per individual is known, such as wood rats (*Neotoma* spp.; Cameron & Rainey 1972, Cranford 1977) or gopher tortoises (*Gopherus polyphemus*; McCoy & Mushinsky 1992), counts of burrows may be more accurate than estimating densities using transect or recapture methods. Especially in studies of animals that are difficult to track, or in rapid assessments, density can be more quickly and accurately estimated by counting the number of burrows in a given area and dividing by the mean number of burrows used by an individual.

Population density in a given habitat depends upon a number of variables, including available burrow sites, predation, competition, and food resource availability. For many Neotropical mammals, we still cannot answer even basic questions about their natural history. To increase our knowledge about food requirements, seed predation and dispersal, and possible impacts on plant communities, we depend on thorough field observations. Direct observations of foraging and feeding behavior in pacas are very difficult, often resulting in low sample sizes and an incomplete picture of which resources they are using. Food items eaten by pacas have been identified in several Neotropical habitats based on observations in captivity (Kraus *et al.* 1970, Matamoros 1980, Smythe & Brown de Guanti 1993), free-range pacas (Smythe 1970, 1978; Gallina 1981; Marcus 1984; Smythe *et al.* 1985), or stomach contents of sacrificed animals (Collett 1981).

One way to obtain more information about food items utilized by pacas would be to identify unique marks left on food remains. Collett (1981) suggested that single incisor marks of $\geq$ 4 mm width on food items indicated manipulation by pacas. In most Neotropical forests, however, pacas occur sympatrically with the similarly sized diurnal rodent *Dasyprocta variegata* (*i.e.,* Smythe 1970, 1978, 1983; Emmons 1984, 1987; Glanz 1985, 1990; Smythe *et al.* 1985; Eisenberg 1989, 1990). We measured incisor widths of 107 pacas and 128 *D. variegata* to determine if we could discriminate between food items consumed by each rodent based on teeth marks left on seeds, fruits, nuts, and other food items. Applying this simple criterion allowed us to identify 33 plant species used by pacas. By providing further insights on spatial use, population density, and food resource utilization of pacas in Costa Rica, and by introducing two new field techniques, we hope to contribute to future study and protection of this and other endangered species.

MATERIALS AND METHODS

STUDY SITE.—Our study was conducted near the Pacific coast of Costa Rica (Hacienda Baru; 83°52′N, 9°15′W) in a tropical lowland wet forest reserve (Holdridge 1947). The average annual rainfall between 1981 and 1994 was 4601 mm (range: 3832–6018 mm) with a pronounced rainy season from May to October. Average daytime temperature was 32.5°C (range: 27–35°C), and average nighttime temperature was 24.5°C (range: 21–26°C). The reserve encompasses 200 ha of primary and secondary forest, including *ca* 5 ha of abandoned cacao plantations and other fruit trees such as mango, pejiballe, plantain, and starfruit. The terrain consists of steep ridges, ranging from 30 to 255 m above sea level, cut by small streams and gullies. Pacas have been subjected to heavy hunting pressure in the surrounding area, but have been protected from hunting within the reserve for about ten years.

RADIOTELEMETRY AND HOME RANGE ESTIMATION.—We trapped pacas by excavating them from their burrows and anaesthetizing them with an intramuscular injection of ten percent ketamine hydrochloride. After recording sex and body weight, individuals were fitted with 38-g VI-2 radio collars (Holohil Systems Ltd., Ontario, Canada) and released at the capture site after the anesthetic had worn off. Radio signals were tracked with TRX-1000S receivers (Wildlife Materials Inc., Carbondale, Illinois) and four-element Yagi hand antennae with affixed compasses. Pacas initially were followed for several hours each night for about one week, to determine how frequently we had to locate a given animal without losing it. We located animals by triangulation from fixed points approximately every 20 min from *ca* 1700 h until *ca* 0730 h, which encompassed their main activity period (Kraus *et al.* 1970; Glanz 1985; H. Beck-King, pers. obs.). The accuracy of triangulated location points was ± 5°. An 8.2-kg adult female was captured on 4 June 1994, and radio tracked over 26 nights between 13 June and 6 October, with a total observation time of 306 h and 767 location points. A 4.8-kg juvenile male (*ca* 17 weeks old; Collett 1981) was captured on 29 August 1994, although the mother escaped. This juvenile male was tracked for ten nights between 8 September and 6 October, with a total observation time of 120 h and 483 location points.

We used the adaptive kernel method (Worton 1989) in the program CALHOME (Kie *et al.* 1996) to estimate the size and shape of home ranges (95%) and core centers (50%). We use the term core center instead of territory because we found no evidence of territorial exclusion. The amount of overlap in the area utilized by the two pacas was calculated with a digital perimeter (Gebr. Haff, 320E, Pfronten, Germany).

POPULATION DENSITY.—We used two methods to estimate population density: (1) counting the number of burrows in the area and dividing by the mean number of burrows used by an individual; and (2) transect census procedures. Leopold (1972) reported that pacas use several burrows, but there are no published data on the actual number of burrows used by individual pacas over a given time period. Our telemetry data is the first attempt to accurately quantify the mean number of burrows used by a paca. Since both animals used three to four burrows at a time, abandoning previous burrows when new ones were established, we used 3.5 as the average number of burrows per individual. To obtain a density estimation based on the number of burrows, we divided the number of burrows found in 12 ha by 3.5. In order to discriminate between active burrows used by other scansorial animals such as *Dasypus novemcinctus* and *Dasyprocta variegata,* we only counted burrows from which we observed a paca escaping, or in which we found paca hair or footprints.

We also estimated the population density in the reserve using two strip census techniques at night, those of King (Leopold 1933), based on mean sighting distances, and Kelker (1945), based on perpendicular distances from the transect. Assumptions and possible biases associated with these methods have been critically evaluated elsewhere (Robinette *et al.* 1974, Cant 1977, Glanz 1985, Chapman *et al.* 1988, Wright *et al.* 1994, Rudran *et al.* 1996). Transect censuses are currently the best methods of estimating densities for "trap-shy" birds and mammals, even with their inherent biases toward underestimating population densities.

Transect surveys were performed along two trails measuring 1.7 and 3.2 km long, within both primary and secondary forest that included a cacao plantation abandoned for seven years. The transect was walked at an average speed of 0.8 km/h, between 1800 and 0300 h. Using headlamps, the bright yellow–orange eye reflections that distinguish pacas from other nocturnal animals (Emmons 1984, Voss & Emmons 1996) were visible up to 30 m away. Between May and September 1994, a total of 12 transect censuses were completed; total sample time was 56 h with a total length of 67.2 km. Time, habitat type, behavior, the distance between the animal and the observer, and perpendicular distance from the transect to the animal when first sighted were recorded.

FOOD RESOURCE UTILIZATION.—We used two methods to determine food resource utilization by pacas: (1) collecting food items from the forest floor to determine if they were handled by pacas based on teeth marks; and (2) analyzing fecal and digestive tract samples from the study area.

To determine if single incisor marks on food remains could be used to identify food resources utilized by pacas, we compared the width of the upper and lower incisors of 107 pacas with 128 *D. variegata* (following Wilson & Reeder's [1993] taxonomy in which *D. punctata* is synonymous with *D. variegata*) from Neotropical specimens in the

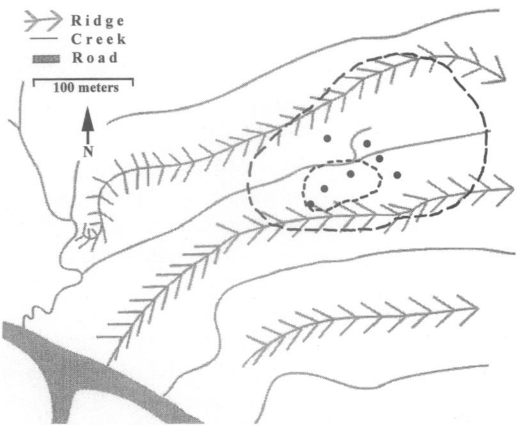

FIGURE 1. Home range and core center (adaptive kernel method) of a juvenile paca for 10 nights. The estimate is based on 483 location points. The large dashes indicate the 95 percent home range, and the small dashes indicate the 50 percent core center. Burrows used by the animal are indicated as circles.

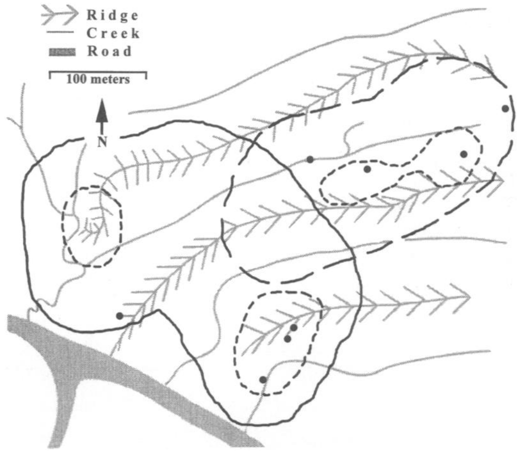

FIGURE 2. Home range and core center (adaptive kernel method) of an adult female paca before and after a shift in home range. Each home range is based on 13 nights (355 and 432 location points, respectively). The first 95 percent home range is indicated by a solid line, the new home range after the shift is indicated by large dashes, and 50 percent core centers are denoted by small dashes. Burrows used by the animal are indicated by circles. Notice the separate core centers.

National Museum of Natural History, Washington DC. Measurements were made only on adult skulls in which the third molar was fully erect using calipers accurate to ± 0.01 mm, and were compared using a *t*-test.

From March to October, we collected all food remains with individual incisor marks of > 4 mm. Specimens were stored in alcohol and identifications were later verified at the Herbario de la Universidad de Costa Rica or the Herbario Nacional de Costa Rica, San Jose.

Fecal samples containing paca hairs were examined for identifiable food fragments. We analyzed four samples (50-, 82-, 11-, and 14-g wet weight): two found in streams and two on the forest floor. We also found a freshly dead paca from which we removed the contents of the entire digestive system (1.1-kg wet weight). Samples were stored in 15 percent formaldehyde and analyzed under a microscope for seed, leaf, fruit, insect fragments, and endoparasites.

RESULTS

RADIOTELEMETRY AND HOME RANGE ESTIMATION.—The mean home range of the juvenile male was 1.49 ha (SE ± 0.24, N = 10 nights) with a core center mean of 0.22 ha (SE ± 0.05, N = 10 nights), located along a small stream bounded by two small ridges (Fig. 1). This animal used seven burrows during the study period, three inside the core center and four outside (but still within) its home range.

For the first 13 nights, between 13 June and 9 August, the home range of the adult female extended over three ridges and contained two separate core centers. Mean home range size was 3.44 ha (SE ± 0.30, N = 13 nights) with a mean core center area of 0.67 ha (SE ± 0.07, N = 13 nights). The female used four burrows, three within the eastern core center and one outside of the two core centers (but still within its home range). Sixty-seven percent of its activity period was spent in the western core area, in which no burrows were located but food resources such as *Persea americana, Virola guatemalensis, Ficus* spp., *Mangifera indica,* and *Inga marginata* were abundant. After 9 August, we detected a shift in the location of the adult female's home range to the more northeastern part of the forest (Fig. 2). This shift coincided with the end of fruit production in five tree species within its previous foraging area. In the new area, different fruits had become abundant, such as *Protium panamense, Maripa nicaraguensis,* and *Spondias purpurea.* From 12 August until the end of the study on 6 October, we tracked the adult female for another 13 nights. Its new mean home range was smaller than the first, measuring 1.76 ha (SE ± 0.24, N = 13 nights) with a mean core center area

TABLE 1. *Comparisons among relative population densities (individuals/km²) of* Agouti paca *from six Neotropical sites employing several methods.*

Reference	Country	Method	*A. paca*/km²
Eisenberg *et al.* (1979)	Venezuela	Track frequency	25
Charles-Dominique *et al.* (1981)	Guatemala	Strip census (King)	30
Collett (1981)	Colombia	Collecting	84–93
Terborgh (1983)	Peru (Cocha Cashu)	Strip census (King)	24
Glanz (1985)	Panama (BCI)	Strip census (King)	40
Smythe *et al.* (1985)	Panama (BCI)	Recapture	70
Emmons (1987)	Peru (Cocha Cashu)	Strip census (King)	3.5
This study (1995)	Costa Rica	Strip census (King)	70
		Strip census (Kelker)	67
		Burrow density	93

of 0.19 ha (SE ± 0.01, N = 13 nights). This new home range overlapped that of the juvenile male and contained two almost separate core centers connected by a small corridor. The adult female maintained a burrow in each of the core center areas and two other burrows within the home range but outside of core centers.

Between 8 August and 6 October, we were able to radio track both pacas simultaneously for eight nights. The home range areas of both animals overlapped by 74 percent, and core centers overlapped by 46 percent. Two of the five burrows of the juvenile male were now located inside the core area of the adult female, whereas one of the female's burrows was in the core center of the juvenile male. The mean distance between the burrows of both animals was 75 m.

During the first week of our telemetry study, the adult female maintained three burrows and in the second week established a fourth. After the home range shift, the female used four burrows during the first two weeks. The juvenile male used three burrows in the first two weeks, but later utilized four different burrows. Based on these findings, we estimated the average number of burrows maintained by a single animal as 3.5.

POPULATION DENSITY.—In the census of 12 ha, we found 39 paca burrows which translated to 325 burrows/km². Dividing by 3.5 we obtained an estimated density of 93 individuals/km². During transect censuses we observed a total of 65 pacas. The population estimation using King's method was 70 individuals/km² and that using Kelker's method was 67 individuals/km² (Table 1).

FOOD RESOURCE UTILIZATION.—The mean width of the upper incisors in museum paca specimens was 4.3 mm (SE ± 0.03, range: 3.45–5.50, N = 107), and that of the lower incisors was 4.1 mm (SE ± 0.03, range: 3.1–5.2, N = 107). The mean for the upper incisors of *D. variegata* was 3.2 mm (SE ± 0.025, range: 2.6–3.9, N = 128), and that for the lower incisors was 3.0 mm (SE ± 0.025, range: 2.1–3.8, N = 128). The width of the upper incisors was significantly different between the two species ($P \ll 0.01$, t = 22.674) as was the width of the lower incisors ($P \ll 0.01$, t = 21.933). Furthermore, of the 128 *D. variegata* skulls measured, none had incisors of 4 mm or wider. Hence, using incisor marks of > 4 mm as a criterion, we were able to identify food consumed by pacas.

We found 33 plant species utilized by pacas (Table 2). The most frequently utilized food resources were fruits of two nonnative cultivars, *Theobroma cacao* and *M. indica,* and of two native trees, *Brosimum utile* and *Licania platypus.* Fruits of these native trees were available in various parts of the forest throughout the seven–month study period. Several fruits such as *M. indica, Spondias* spp., *Ficus* sp., and *Passiflora* spp. were almost completely eaten, including the skin; however, in a number of other fruits such as *Musa* sp., *T. cacao,* and *B. utile,* pacas generally peeled away the skin and removed the fleshy pulp. In other cases, such as in *P. americana, M. indica,* and *M. nicaraguensis,* pacas ate the fruit flesh, then crushed and ate the seeds. Pacas not only removed the outer skin from fruits of *Scheelea rostrata* to eat the oily flesh, but they also opened the extremely hard, woody seed coat to consume the endosperm. In addition, pacas partially ate *M. indica* seedlings, and flowers of *Musa* sp. In the four fecal samples, we discovered fragments of monocotyledonous and dicotyledonous leaves. Three fecal samples revealed a total of 173 undamaged seeds of seven morphospecies. Fruit flesh and skins, plant fibers, and remains of ants and lepidopteran larvae were found as well.

TABLE 2. *Food resources utilized by* Agouti paca *during the rainy season in a Pacific lowland rain forest in Costa Rica. Abbreviations: flower = FL; seed = S; seedling = SL; fruit flesh = F; skin = SK.*

FAMILY Species	Common local name	Utilized food items
ANACARDIACEAE		
Mangifera indica	Mango	SK, F, S, and SL
Spondias mombin	Jobo	SK, F, and S
S. purpurea	Jocote	SK and F
BOMBACACEAE		
Quararibea asterolepes	Molenillo	SK and S
BURSERACEAE		
Protium panamense	Tostado	S
CHRYSOBALANACEAE		
Licania operculipetala	Camarón	S
L. platypus	Sonsapote	F and S
Licania sp.		F and S
CONVOLVULACEAE		
Maripa nicaraguensis	Tapa Dulce	F and S
EUPHORBIACEAE		
Hura crepitans	Javillo	SK and S
LAURACEAE		
Persea americana	Aguacate	F and S
Nectandra sp.	Quizarra	S
LEGUMINOSAE		
Inga marginata	Cuajiniquil Negro	F and S
Inga sp.	Guaba	S
MELASTOMATACEAE		
Bellucia sp.		F and S
MORACEAE		
Batocarpus cf. *costaricensis*	Lechillo	F and S
Brosimum alicastrum	Ojoche	F and S
B. utile	Lechoso	SK, F, and S
Ficus sp.	Higuerón	SK, F, and S
MUSACEAE		
Musa sp.	Platanillo	F and FL
MYRISTICACEAE		
Virola guatemalensis	Fruta Dorada	F
OXALIDACEAE		
Averrhoa carambola	Carambola	F and S?
PALMAE		
Bactris gasipaes	Pejivalle	F and S
Scheelea rostrata	Palma Real	SK and S
PASSIFLORACEAE		
Passiflora vititelia	Granadilla	SK, F, and S
Passiflora coccinea	Granadilla	SK, F, and S
RUBICEAE		
Tocoyena cf. *pittieri*		F
SAPOTACEAE		
Pouteria cf. *foelata*	Zapote	S
Pouteria sp.	Zapote	F and S

TABLE 2. *Continued.*

FAMILY Species	Common local name	Utilized food items
STERCULIACEAE		
Theobroma cacao	Cacao	F and S
Theobroma sp.	Cacao silvestre	F and S?
Herrania purpurea	Cacao de Mico	F and S?
TILIACEAE		
Apeiba tibourbou	Peine de Mico	F and S?

We found a total of 243 seeds from three different species in the dissected digestive tract, 185 of which were small seeds (1.5-mm diameter) of a single species. Although we attempted to identify the seeds by comparing them to herbarium specimens from the Herbario de la Universidad de Costa Rica, the Herbario Nacional de Costa Rica, and INBIO, identification was not possible. As in the fecal samples, we found fragments of monocotyledonous and dicotyledonous leaves. We also discovered three endoparasitic nematode species: *Bradypostrongylus panamensis* and *Trichuris muris* throughout the digestive system and *Trichostrongylus axei* (a blood sucking species) in the caecum of the pacas (D. T. Clark, pers. comm.).

DISCUSSION

HOME RANGE.—The juvenile male maintained only one core center throughout the month of tracking (although on some individual nights it had two separate centers of activity), and its foraging was restricted around its den area. The adult female consistently centered its activity in two areas, sometimes maintaining burrows in one and foraging in another. The female shifted its home range in August, probably in response to changing fruit availability. Interestingly, after the shift into a new area the adult utilized a large proportion of the area occupied by the juvenile male. Since juveniles tend to remain with their mothers for up to a year (Collett 1981, Smythe & Brown de Guanti 1993), our collared adult female probably overlapped another adult's home range as well. The large amount of overlap in home ranges (and especially core centers) by these animals suggests that intraspecific competition, at least between females, may not be a dominant force in home range selection. Marcus (1984) reported similar spatial behavior by females in Panama. We occasionally observed up to five untagged pacas also foraging in this area. This was not surprising considering the high abundance of food resources.

The only other radiotelemetry study conducted on pacas was on Barro Colorado Island (BCI), Panama (Marcus 1984). In that study, Marcus estimated home range sizes, based on a combination of radiotelemetry, live trapping, and direct observation, as 2.3 ha for adult females and 0.7 ha for juvenile males. For comparison, we reanalyzed our home range estimates using the minimum convex polygon method. We found our adult female to have a smaller average home range (1.7 ha) and our juvenile male to have a larger (1.8 ha) one than he found in Panama. These differences in home range sizes between BCI and our study may be due to different fruit abundances, or simply may reflect the methods used.

POPULATION DENSITY.—Because pacas are threatened or endangered in many areas, it is important to estimate density quickly and accurately. Assessing density directly by transect census requires a large investment of time for results that may be biased. Rapid assessment techniques are becoming more frequently needed, especially in threatened tropical areas in which accurate density estimations for many endangered species are essential to management and conservation decisions.

Our telemetry data on an adult female and a juvenile male suggest that pacas use between three and four burrows at a time. Pacas form monogamous pairs, but adults have never been observed occupying the same burrow (Smythe 1970; Collett 1981; Marcus 1984; H. Beck-King, pers. obs.). Although we were unable to track adult males, they are known to have home range sizes similar to females (Marcus 1984, Smythe *et al.* 1985). It seems reasonable to assume that male and female pacas also use a similar number of burrows. If we multiply the mean number of burrows used by our individuals (3.5) by the population density estimated using King's transect method (70 individuals/km^2), we would expect 245 burrows/km^2—almost 25 percent less than found in our census (325 burrows/km^2). We estimated population density based on burrow number to be 93 individuals/km^2. Since Emmons (1984) and Glanz (1985) have found that transect methods underestimate density by up to 50 percent, we believe that our method based on burrow density may give a more accurate estimate of population density. As in the case of gopher tortoises (McCoy & Mushinsky 1992), however, it is quite possible that the number of burrows used by pacas changes with habitat and microhabitat variables. Hence, it is important to point out that because there are no previous data for pacas on burrow density or the number used per individual, our estimated mean must be tested in other areas.

Our population density estimates were among the highest compared to other studies of pacas (Table 1). Emmons (1987) recorded the lowest density of pacas in Cocha Cashu, Peru, of only 3.5 individuals/km^2. Emmons (1987) and Janson and Emmons (1990) suggested two major factors to explain such low density. First, during the rainy season, up to 30 percent of the forest habitat available for burrow-dwelling animals is covered by water. Second, Cocha Cashu has a high density of felids that may regulate medium-sized prey species in a top-down fashion. Terborgh (1983) had reported a much higher relative density of pacas (24 individuals/km^2) at the same site. This difference in density between years may be due to variation in fruit availability or rainfall. Collett (1981) reported a relatively high density (between 84 and 93 individuals/km^2) in three gallery forests of Colombia. Such forests are thought to be the most suitable habitat for pacas (Smythe 1978, 1983; Collett 1981; Perez 1992). Using King's transect method, Glanz (1985) estimated 40 individuals/km^2 on BCI, while Smythe *et al.* (1985) estimated a relative density of 70 individuals/km^2 on BCI employing recaptures over a seven-year period. Estimates based on recapture data also may be biased, due to avoidance of traps by the animals (Collett 1981, Smythe *et al.* 1985). Since BCI is a small island (1500 ha) on which larger predators such *Panthera onca* and *Felis concolor* are absent (Eisenberg *et al.* 1979; Emmons 1984, 1987; Glanz 1985, 1990), prey species such as pacas are thought to have reached higher densities than in areas in which top predators are present (Terborgh & Winter 1980, Wright *et al.* 1994). Wright *et al.* (1994) challenged the widely accepted opinion that high densities on BCI are due to a lack of top predators. They concluded that most previous censuses there were conducted in areas in which animals were habituated to humans, leading to overestimates of herbivore densities. In a comparison of sites with and without predators, they found no significant difference in the mean densities of most herbivores. Several studies have suggested that resources limit herbivores and frugivores (Smythe 1970; Glanz *et al.* 1985; Smythe *et al.* 1985; Terborgh 1986a, b). Terborgh and Wright (1994) found equal rates of seed and seedling predation on *Dipteryx panamensis* at both Cocha Cashu and BCI, supporting Wright's hypothesis. Further studies including supplementation and removal experiments are needed to determine whether and when predation or resource limitation is the more dominant factor in determining herbivore densities.

Both factors may have contributed to the high density of pacas at our study site. Food resources were abundant from abandoned cacao plantations and fruiting trees within the reserve, and large predators were mostly absent. In addition, three streams carry water through the broken terrain, offering an abundance of suitable burrow sites throughout the forest.

What impact might such a high paca density have on forest dynamics and species composition as a result of seed dispersal and predation? In a study of the effects of low densities of pacas and other herbivores, Dirzo and Miranda (1991) reported that dramatic defaunation in Los Tuxtlas, Mexico, may have reduced plant species diversity by up to two-thirds. Further studies are needed to evaluate the ecological role of pacas as seed predators and dispersers, and the consequences of local extinction on forest dynamics.

Food resource utilization.—Direct observations of feeding by pacas are difficult in the field. Our method of identifying food resources based on incisor marks of > 4 mm is a practical, if conservative, approach. Using this method, we cannot distinguish between subadult pacas and adult *D. variegata,* or identify food items that are too soft or completely consumed. Nonetheless, this method has proven to be an effective approach to catalog foods consumed by adult pacas. A comparison of food items utilized by pacas in our study and other investigations in the Neotropics revealed that 61 percent of 33 plant species we found were new records (Smythe 1970, 1978; Matamoros 1980; Collett 1981; Gallina 1981; Marcus 1984; Smythe *et al.* 1985). The hard-shell palm nuts of *S. rostrata* were thought to be too hard for pacas to open (Marcus 1984), especially since they rarely use their forelimbs to hold and manipulate food items. On several occasions, however, we and Smythe (pers. comm.) have observed pacas using the forelimb to open Scheelea nuts. Although Howe and Kerckhove (1981) had reported that *Virola surinamensis* fruit was eaten only by frugivorous birds and one monkey, Howe (1993) found that pacas eat the seeds of *V. nobilis*; we found that pacas also eat *V. guatemalensis* fruit.

The high number of seeds (a total of 416) in the fecal samples and digestive tract strongly suggests that pacas may be important seed dispersers or predators. Seed survival and growth depend to some extent on distance from their parent tree (Hubbell & Foster 1990), and on intraspecific seed density (Howe 1980). Therefore, to maximize their fitness, plants have evolved traits for dispersal. Howe (1989) classified frugivores weighing < 3 kg as scatter-dispersers, and animals with a body mass of > 3 kg as clump-dispersers. Pacas, which can weigh up to 12 kg (Nowak 1991, Perez 1992), may not fit this pattern. Although our pacas produced feces with high numbers of seeds, their predator avoidance behavior leads them to defecate into streams (Collett 1981, Marcus 1984, Smythe & Brown de Guanti 1993). In fact, half of our samples were found in creeks in which secondary dispersal by water would separate seeds and scatter them further than by primary dispersal. Tapirs (Janzen 1981), Hippopotamuses (Crawley 1983), and other semiaquatic animals that defecate mainly in water, also may present exceptions to Howe's classification.

In conclusion, our results on space use, relative density, and resource utilization provide further insight into the ecology of pacas, and could benefit the conservation and management of this species. Our two suggested methods—estimating population density by using the number of burrows divided by the mean number of burrows used and identifying food items by incisor marks of > 4 mm—are useful techniques that could aid future research as an alternative to conventional methods and perhaps contribute to the conservation of *A. paca* in the Neotropics.

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