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DENSITY, BIOMASS, AND MOVEMENT ESTIMATES FOR MURID RODENTS IN MOSSY FOREST ON MOUNT ISAROG, SOUTHERN LUZON, PHILIPPINES

Danilo S. Balete[1,2] & Lawrence R. Heaney[1]

[1]Department of Zoology, The Field Museum, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605, U.S.A.
[2]Department of Biological Sciences, University of Illinois at Chicago, 845 W. Taylor Street, Chicago, Illinois 60607, U.S.A.

Abstract. A mark-and-recapture study of small mammals in mossy forest (c. 1600 m elevation) on Mt. Isarog, southern Luzon island, Philippines, appears to be the first of its kind in this habitat. Rapid disappearance of nearly all lowland forest in southern Luzon has left Mt. Isarog as a crucial sanctuary for the fauna. Rainfall during the five-month study totaled c. 8800 mm, the highest recorded in the Philippines, and was five times the total during the same period in the lowlands. A total of 77 individuals was captured, marked, and released, representing six species; all six are Philippine endemics, and three are threatened species known only from Mt. Isarog. Numerical dominance by two omnivorous species was marked; three vermivore/insectivores and a frugivore/herbivore were less common. Density totaled 20.1/ha, one of the highest levels recorded in tropical forest. Biomass totalled 1555 g/ha, with individual species ranging from a high of 591 g/ha to a low of 138 g/ha. Home range size was estimated to be 0.22 ha for *Apomys musculus* and 0.41 ha for *Rattus everetti*; female *R. everetti* moved significantly further than males, and *R. everetti* moved significantly further than *A. musculus*. Predation by a carnivore, probably *Paradoxurus hermaphroditus*, was documented on *Apomys musculus*, *Phloeomys cumingi*, and *Rattus everetti*. *Accepted 9 September 1997.*

Key words: *Small mammals, murids, Philippines, mossy forest, biomass, density, home range, predation, endemic species, conservation.*

INTRODUCTION

Tropical forests harbor the richest and most diverse biotas on earth; they also comprise one of the world's most threatened ecosystems (Wilson 1988). If the rates of forest destruction that characterized the last two decades were to continue, some countries in the biologically-rich Indo-Malayan realm, including the Philippines, will loose virtually all of their remaining forest cover within the next ten years (Dinerstein & Wikramanayake 1993). What remains in tropical Asia is likely to be in isolated areas, especially at higher elevations, because the forest in such places is of low stature and therefore of little value for timber production, and because the steepness of the terrain makes subsistence farming difficult. The direct effects of deforestation are now emerging in the Philippines; in addition to severe economic repercussions related to increased flooding, droughts, erosion, and siltation (Myers 1988), some species are now presumed extinct and many more are threatened, especially birds (Diamond 1990, Goodman & Gonzales 1990, Dickinson *et al.* 1991, Tabaranza & Mallari, 1997) and mammals (Cox 1987, Heaney & Heideman 1987, Heaney & Utzurrum 1991, Utzurrum 1992, Heaney 1993, Oliver *et al.* 1993, Heaney *et al.* 1997). With practically all lowland forests gone, only the montane and mossy forests remain relatively intact (Development Alternatives, Inc. 1992). Fortunately, montane tropical habitats often harbor large numbers of endemic mammal species (e.g., Goodman *et al.* 1997, Patton *et al.* 1990), and this is true in the Philippines (Heaney *et al.* 1997, in press; Rickart *et al.* 1991). Typically, these species are even less well known than species in the lowlands, where information is generally viewed as seriously inadequate (Fleming 1975, French *et al.* 1975, Heaney 1993, Heaney *et al.* in press, Timm 1994, Glanz 1982, Ryan *et al.* 1993). In the Philippines, studies of nonvolant montane mammals have provided some basic information on relative abundance, habitat use, reproduction, and food habits (e.g., Heaney *et al.* 1989, in press; Heaney & Rickart 1990; Heideman *et al.* 1987; Rickart *et al.* 1991, 1993; Rickart 1993; Ruedas *et al.* 1994), but have not included the mark-and-recapture data that are necessary to estimate density, movement patterns, home range size, and population dynamics.

The objective of this study was to conduct a mark-and-recapture analysis of small mammals in mossy rainforest on Mt. Isarog in southern Luzon. Mt. Isarog contains the largest and best-protected patch of forest in southern Luzon, and is exceptional in having three endemic species of small mammals (*Archboldomys luzonensis*, *Chrotomys gonzalesi*, and *Rhynchomys isarogensis*; Musser 1982, Musser & Freeman 1981, Rickart & Heaney 1991), all of which are recognized as threatened by the IUCN due to loss of habitat (Baillie & Groombridge 1996, Heaney *et al.* 1997). Elevational ranges, habitat associations, community composition, and food habits of all of the small mammals were moderately well known at the start of this study (Rickart *et al.* 1991). This is the first mark-and-recapture study of native small mammals in the Philippines, and appears to be the first in tropical mossy forest habitat world-wide.

The data presented here were obtained during a six-month field season, and so do not represent a full annual cycle. Moreover, rainfall during the study was high (estimated at 8800 mm per year, as discussed below), inhibiting research activities. Thus, we view our results as initial estimates; however, the rarity of such data, and the endangered status of the habitat and species, make even rough data quite valuable.

STUDY AREA

The Philippine Archipelago consists of at least 7,000 islands of varied sizes and geological histories (Defant *et al.* 1989; Mitchell *et al.* 1986; Heaney 1986, 1991; Hall 1996). The mammalian fauna on these islands is remarkably diverse and high in endemics. Over 170 species of native terrestrial species are known, of which about 65% are endemic; among murid rodents, 95% of the species are endemic, often restricted to only one or a few islands (Heaney *et al.* in press, Musser & Heaney 1992, Heaney 1993).

Mt. Isarog is an extinct volcano located in Camarines Sur Province, southern Luzon at 13°40' N, 123°23' E. There is no record of volcanic eruptions by Mt. Isarog during historical times (Adams & Pratt 1911, Pratt 1915). The climate of Mt. Isarog is characterized by the absence of a distinct dry season, but with a pronounced wet period with maximum rain during December and January (Kintanar 1984). Mean annual precipitation is 2350 mm in the adjacent lowlands (Manalo 1956). At our study site, precipitation of nearly 2 m was recorded in a single month (December; an average of 73.7 mm daily), largely due to heavy rains borne by frequent stormy weather and several typhoons (Balete 1995). The highest daily rainfall recorded during this study was 143.7 mm on 27 December 1993. The driest month was February, with a total of 567.2 mm. Compared with the lowlands, based on the records at a weather station near sea level in Camarines Sur State Agricultural College (CSSAC), Pili, Camarines Sur, the total precipitation in the mossy forest was about five times higher than near sea level (Balete 1995).

Air temperature from March to May was 10°–23.9°C at 1700 m (Rickart *et al.* 1991). Average temperatures at the study site ranged from 12.8°C (February 1994) to 20.7°C (April 1991). The coldest temperature recorded at the study site was 10°C (06 February 1994) while the warmest was 24.5°C (23 March 1994). During the same period at Naga City near sea level, the average temperatures ranged from 20.9°C (February 1994) to 33.5°C (April 1994), with the coldest temperature recorded on 17 February 1994 (17°C) and the highest on 27 April 1994 (35.5°C).

The rapid loss of forest cover seen throughout southern Luzon was evident on Mt. Isarog, where the remaining primary forest consists mainly of the relatively intact montane (from c. 1000 to 1500 m elevation) and mossy forest (from c. 1500 m to the peak at 1996); (Goodman & Gonzales 1990, Rickart *et al.* 1991, Balete 1995). The study area was in mossy forest, at c. 1650 m. The soil was weathered volcanic tuff covered with a thick layer of organic debris and a spongy root layer. The forest canopy was 9 to 12 m in height. Trees and understory vegetation were covered with a thick layer of mosses, epiphytic ferns (e.g., *Huperzia*, *Hymenophyllum*, and *Trichomanes*) and orchids from trunks to branches. Climbing pandans, *Freycinetia* spp. (Pandanaceae), on tree trunks were also abundant. Vegetation analysis on the trapping grids indicates the predominance of *Eugenia* (= *Syzygium*, Myrtaceae) spp. at the study site (Heaney *et al.* in prep.). Other abundant species include *Cyathea* spp. (Cyatheaceae), *Tricalysia fasciculata* (Rubiaceae), and *Elaeocarpus argentes* (Elaeocarpaceae). Forest floor vegetation included herbaceous plants (e.g., *Languas scabra*, *Sarcandra glabra*), ground orchids, and rattans (*Calamus* spp.).

METHODS

Trapping from late December 1993 until mid-February 1994 was conducted on two grids that were c. 120 m apart, within the same elevational band, 1600–1650 m, in mossy forest. Initially, each square trapping grid consisted of four sub-grids with 36 trap stations in six rows and six columns. Distance between adjacent trapping stations was 5 m. Each sub-grid covered an area of 625 m^2 for a total of 4900 m^2, including the 20 m strips that separated the sub-grids. We also trapped a small number of individuals adjacent to our camp, 100 m from the nearest point on a grid. After trapping each grid once in December 1993/January 1994 (1150 trap-nights on each of the two grids), it was evident that the movements of small mammals were not constrained by the streams bisecting the sites in many places, and home range areas were much larger than anticipated. In mid-February 1994, the inter-trap distance in the grid at Site 1 was expanded to twice the original distance, increasing the area encompassed by the expanded grid to 14400 m^2, and the grid at Site 2 was removed. Four trapping sessions were then conducted (24–26 February, 12–15 March, 24–27 March, 26–27 April 1994). All data reported here are from the 24 February until 25 May 1994 period. Even with the increase in grid size, some individuals of two species (*Apomys musculus* and *Rattus everetti*) had home ranges larger than the grid, and so data on movement of small mammals should be taken to indicate minimum estimates of home range size.

We used cage traps measuring 27 x 9 x 9 cm manufactured locally of welded wire or chicken wire. Traps of this construction were used previously in the field on Luzon with satisfactory results (Danielsen *et al.* 1993). Two types of baits were used throughout the trapping study following Rickart *et al.* (1991). During the first two days of the four-day trapping schedule, traps were baited twice daily with thin strips of fried coconut coated with peanut butter. During the last two days of trapping, baits were replaced with live earthworms tied to the bait hooks with very fine wire. At the end of each four-day trapping session, the traps were cleared of baits before closing them. Traps remained on their respective stations throughout the duration of this study. Traps were checked three times daily: dawn, noon, and after dusk.

Two sizes of Michel clips, 11 x 2 mm and 14 x 3 mm, were used for ear-tagging animals (Le Boulenge-Nguyen & Le Boulenge 1986). The clips were engraved with unique two-letter codes on smaller clips and a unique letter and number code (two digits) on larger clips. At first capture, each individual was identified to species, weighed, sexed, and examined for its reproductive condition before being tagged and released. Upon recapture, each animal was checked for identifying ear tags and weighed, and trap location, date and time of capture, and bait were noted.

During our five-month study period, there was no evidence of population turnover due to births, immigration, or migration (reproduction occurs at a different time of year; Balete 1995, Heaney *et al.*, in prep.). Thus, a closed population was assumed and the modified Lincoln-Petersen index was used to estimate population size, with 95% confidence interval, following White & Garrot (1990). However, due to the extremely high precipitation, deaths of trapped animals occurred, including four individuals of *Apomys musculus*, one of *Archboldomys luzonensis*, and one of *Rattus everetti* (overall, the mortality rate was c. 15%). These were not included in the computation of the Lincoln-Petersen estimator, but instead were added to the estimated population size for the period when the deaths occurred. Population size was estimated for each of the four trapping sessions defined above; the relatively small confidence intervals for the estimates (in Balete 1995) suggest that population estimates for *Apomys musculus* and *R. everetti* are reliable and are consistent with the demographic closure assumption of the modified Lincoln-Petersen estimate.

For *Apomys musculus* and *Rattus everetti* (the species in which some individuals had home ranges larger than the grid), the mean distance moved between captures, MDM (Gurnell & Gipps 1989), was used as the width of the boundary strip. Thus, the effective trapping area used to estimate the densities of these two species was $A = [120 \text{ m} + 2(\text{MDM})]^2$. For other species, which had no recorded movement outside of the trapping grids, the total area of 14400 m^2 was used in computing their densities. Density was calculated for each of the four trapping sessions, with density defined as the Lincoln-Petersen estimate of population size divided by the relevant area (Balete 1995). Biomass was derived by multiplying the mean mass (g) of each species during each trapping period by their estimated density (no./ha) for the same period.

Home range was estimated using the Jennrich-Turner Estimator, which assumes a bivariate normal distribution of capture points and an elliptical home range shape (White & Garrot 1990). Points of captures of each animal were plotted on graph paper to determine the x-y coordinates. Calculation of the means, variances, and co-variances of the x and y coordinates followed White & Garrot (1990).

RESULTS

Community Composition. A total of 77 individuals was captured, marked, and released in a span of five months. These captures represent six species of native murid rodents: *Apomys musculus*, *Archboldomys luzonensis*, *Batomys granti*, *Chrotomys gonzalesi*, *Rattus everetti*, and *Rhynchomys isarogensis*. Three of these, *A. luzonensis*, *C. gonzalesi*, and *R. isarogensis* are found only on Mt. Isarog, and the others are Philippine endemics. *Apomys microdon* was not recorded in the study area; its occurrence in 1988 at the same site was at very low densities (Rickart *et al.* 1991, Heaney *et al.*, in prep.). *Crocidura grayi* was not taken in live traps but was sighted. Based on their trophic adaptations, these species can be broadly categorized (Rickart *et al.* 1991) as: omnivore (*A. musculus* and *R. everetti*), granivore/frugivore (*B. granti*) and vermivore/insectivore (*A. luzonensis*, *C. gonzalesi*, and *R. isarogensis*; Table 1).

Density and Biomass. Apomys musculus had the highest estimated population size, with a mean population estimate of 36, followed by *Rattus everetti* with 9, *Archboldomys luzonensis* with six, and *Batomys granti* and *Rhynchomys isarogensis* with a mean size of four (Table 1). Overall, the average number of small mammals captured was 60 (range, 57–67). *Chrotomys gonzalesi* was the least often captured of the species, and it was not possible to estimate its population size.

The total density of small mammals in the mossy forest of Mt. Isarog was estimated to be 20.1 animals/ha (Table 1), almost two-thirds of which was accounted for by the two smallest species, *Apomys musculus* (8.8/ha) and *Archboldomys luzonensis* (4.5/ha). *Rhynchomys isarogensis* and *Rattus everetti* had the lowest estimated densities (2.6 and 1.2 animals/ha, respectively). Sample size was small for several species, so that these should be viewed as rough estimates.

With respect to trophic categories, half of the mean density of small mammals in the mossy forest of Mt. Isarog was comprised of the omnivores *A.*

TABLE 1. Summary of ecological and demographic information on the small mammals on Mt. Isarog, southern Luzon (Rickart *et al.* 1991, Heaney *et al.*, in prep., this study).

Species	Mass (g)	Population Size (range)	Density (no./ha)	Biomass (g/ha)	Trophic Adaptation
Crocidura grayi	10.8 ± 1.0	–	–	–	Insectivore
Apomys microdon	35.1 ± 3.7	–	–	–	Omnivore
Apomys musculus	21.0 ± 1.8	36 (34–42)	8.8 ± 0.66	163.2 ± 21.20	Omnivore
Archboldomys luzonensis	35.4 ± 5.4	6 (4–9)	4.5 ± 1.63	138.5 ± 50.04	Vermivore-Insectivore
Batomys granti	162.2 ± 27.5	4 (3–5)	3.0 ± 0.67	591.5 ± 116.49	Granivore-Frugivore
Chrotomys gonzalesi	135.6 ± 35.3	–	–	–	Vermivore
Rattus everetti	252.9 ± 46.5	9 (7–10)	1.2 ± 0.05	333.3 ± 61.37	Omnivore
Rhynchomys isarogensis	122.5 ± 9.5	4 (2–5)	2.6 ± 1.05	328.4 ± 113.36	Vermivore

TABLE 2. Mean (± SD) and maximum distance travelled between successive recaptures by *Apomys musculus* and *Rattus everetti*. Numbers in parentheses are number of captures; numbers in boldface are maximum distances moved.

Species	N	Small grid	Large grid	Small and large grids
Apomys musculus				
Male	11	43 ± 48.9 (27) **190**	41 ± 34.2 (98) **150**	41 ± 37.6 (125)
Female	12	42 ± 47.4 (20) **191**	46 ± 50.9 (52) **226**	44 ± 49.7 (72)
Both sexes	23	42 ± 47.6 (47)	42 ± 40.7 (150)	42 ± 42.3 (197)
Rattus everetti				
Male	2	50 ± 44.6 (8) **154**	65 ± 68.1 (12) **244**	50 ± 42.8 (20)
Female	3	94 ± 100.1 (11) **228**	89 ± 63.0 (14) **183**	91 ± 79.8 (25)
Both sexes	5	71 ± 77.8 (19)	74 ± 59.7 (26)	73 ± 68.4 (45)

musculus (44%) and *R. everetti* (6%), and over a third was accounted for by the vermivore-insectivores *A. luzonensis* (22%) and *R. isarogensis* (13%). The granivore-frugivore, *B. granti*, accounted for the remaining 15%.

The mean total biomass of small mammals in the mossy forest, estimated to be 1554.9 g/ha (Table 1), was almost equally divided among the species of three trophic categories: omnivores (32%), vermivore-insectivore (30%), and granivore-frugivore (38%). The three largest species had the highest biomass/ha and together accounted for four-fifths of the total estimated biomass: *B. granti* (591.5 g/ha, 38%), *R. everetti* (333.3 g/ha, 21%), and *R. isarogensis* (328.4 g/ha, 21%). Less than a fifth of the biomass was accounted for by the two smallest species, *A. musculus* (163.2 g/ha, 10%) and *A. luzonensis* (138.5 g/ha, 9%). Again, sample size was small for several species, and these data should be viewed as rough estimates.

Movement and Home Range. The mean distance moved between captures (MDM) of *Apomys musculus* was 42 m, with maximum distances of 190 m in males and 226 m in females (Table 2). In *Rattus everetti*, MDM averaged 73 m, with maximum distances of 244 in males and 228 in females. Other species recorded during our study were captured infrequently and showed smaller home ranges. One female *B. granti* trapped five times for three successive days in February had a MDM of only 11 m (range, 5–14 m). A second female of the same species, captured eight times in a span of three months, had a MDM of 44 ± 23.0 m (range, 14–85 m). Among the vermivores, a male *R. isarogensis*, captured thrice in three days, travelled an average of 50 m (range, 40–60 m). A female *A. luzonensis* was recaptured once, within two days from its initial capture, having moved 92 m from the point of its original capture.

An independent t-test comparing the inter-sex differences in MDM in *R. everetti* (Table 3) showed that females moved significantly longer distances than males. This trend was also observed in *A. musculus* (Table 3), in which a difference was present but statistically insignificant. Overall, Table 3 also shows that the difference in MDM between *A. musculus* and *R. everetti* was highly significant. In both species, however, the effect of grid size on MDM was insignificant.

Due to very few recaptures of the vermivorous rodents, home range size was estimated only for *Apomys musculus*, *Batomys granti*, and *Rattus everetti* (Table 4). In both *A. musculus* and *R. everetti*, mean home range sizes of males was only about half that of females, but these differences were not statistically significant (Table 4). Between 20 and 100 % of the home range of one individual overlapped with at least one other individual in both *A. musculus* and *R. everetti*. One female *B. granti* had a home range of 0.11 ha, which overlapped with both *A. musculus* and *R. everetti*.

TABLE 3. Independent t-test comparing MDM (mean distance moved between captures) between males and females of *Apomys musculus* and *Rattus everetti*, between small and large grids, and between these two species. Number of captures, Mean, and SD are given in Table 4. T values and probabilities are for pooled variances.

Species	Variable group	t	df	*P*
Apomys musculus	Sex	−0.583	195	0.561
	Grid size	0.036	195	0.971
Rattus everetti	Sex	−2.097	43	0.042
	Grid size	−0.143	43	0.888
All species	Species	−3.808	240	0.001

Predation. The two species of viverrids which occur throughout the Philippines, *Viverra tangalunga* and *Paradoxurus hermaphroditus*, were recorded previously in lowland, montane, and mossy forest on Mt. Isarog (Heaney *et al.*, in prep.). During this study, the presence of the palm civet, *P. hermaphroditus*, in the mossy forest was further documented with a specimen of a young female which was captured at 1550 m. We also collected scats of small carnivores at several elevations along the trail leading to the trapping sites. Our data indicated only nocturnal activity of the viverrids in the study area. We recorded two attacks on live-trapped *Apomys musculus* at night: a male *A. musculus* lost a leg when it was attacked by a palm civet observed close to the trap at 18:00 h, and another *A. musculus* lost a hind foot.

The composition of predator scats collected inside and outside of the trapping sites indicate the omnivorous feeding habit of these predators. Four scats from 1450 m up to 1600 m elevation contained remains of *A. musculus* (two scats) and *R. everetti* (one scat), bones of a small frog (one scat), insects (Coleoptera and Orthoptera), and flowers and fruits of the climbing pandans (*Freycinetia* spp.; three scats) and fibrous seeds of *Elaeocarpus luzonicus* (Elaeocarpaceae; two scats). Two scats collected at lower elevation (1150 m) contained *Rattus everetti* (one scat) as well as foot bones of an adult cloud rat, *Phloeomys cumingi* (one scat), apparently the first recorded case of non-human predation on this endangered species (Oliver *et al.* 1993).

DISCUSSION

Mossy Forest Habitat. The floristic composition of the mossy forest on Mt. Isarog suggests a plant community that is characteristic of the mossy forests in other parts of the Philippines, such as on Mt. Halcon,

TABLE 4. Mean (± SD) of estimated home range size (in hectares) of small mammals in the mossy forest of Mt. Isarog. Home range ellipse computed using Jennrich-Turner Estimator. Only individuals with at least seven captures were included in the computation. Range is indicated by numbers in boldface. Independent t-test compares inter-sex differences in *A. musculus* and *R. everetti*. T values and probabilities are for pooled variances.

Species	Sex	N	Home range (ha)	t	df	*P*
Apomys musculus	Male	9	0.15 ± 0.128 **0.01 - 0.43**			
	Female	6	0.32 ± 0.197 **0.04 – 0.56**			
	Both sexes	15	0.22 ± 0.174	−1.955	13	0.072
Batomys granti	Female	1	0.105			
Rattus everetti	Male	2	0.20 **0.08 - 0.32**			
	Female	3	0.56 ± 0.378 **0.32 - 0.99**			
	Both sexes	5	0.41 ± 0.343	−1.219	3	0.312

Mindoro (Merrill 1907) and Mt. Pulog, northern Luzon (Merrill & Merritt 1910). The presence on Mt. Isarog of *Cryptocarya*, *Elaeocarpus*, *Eurya*, *Lithocarpus*, *Psychotria*, *Schima*, *Symplocos*, and *Syzygium* further suggests its affinity to the flora of high elevation forests elsewhere in Southeast Asia (e.g., Whitmore 1984, Ohsawa *et al.* 1985). Although the very high precipitation recorded during this study (c. 8800 mm in six months) is the highest reported in the Philippines, exceeding records for a mid-elevation site in the central Philippines (Heideman & Erickson 1987) and for mountainous regions of northern Luzon (e.g., Mountain Province; Manalo 1956), virtually no information on rainfall in mossy forest has been available previously, and we have no reason to believe that Mt. Isarog is exceptional in this respect. The recorded temperatures at the study site of 10°C to 24.5°C are consistent with previous records taken from 1750 m on the same mountain (Rickart *et al.* 1991). This was, on the average, at least 10°C cooler than the lowlands. In general, the floristic and structural characteristics of the forest, as well as climatic factors such as precipitation and temperature, are consistent with those of montane forests in other parts of Southeast Asia (Whitmore 1984).

Density and Biomass. The overall density estimate of 20.1 animals/ha for all species was quite high compared to most available estimates for small mammal faunas in tropical forests. It was considerably higher than estimates for murid rodents in primary lowland forest (3.5 animals/ha) and in grassland (5.5 animals/ha) in peninsular Malaysia (Harrison 1969). Although the density of murids in a tree plantation in Sabah, Borneo was generally higher than on peninsular Malaysia, it came only to about half that of Mt. Isarog rodents (Steubing & Gasis 1989). The murid density on Mt. Isarog was comparable to the estimated rodent density of 18.9 animals/ha in dry tropical forest in Panama (Fleming 1975). Adler (in press) and Adler *et al.* (in press) found densities of 12–43 individuals/ha for *Proechimys semispinosus* on very small (1.7–3.5 ha) islands in Lake Gatun, Panama, indicating higher overall density for the small rodent community.

Even when compared to non-volant small mammals of all taxa, the density of the small mammals in the mossy forest on Mt. Isarog remained higher than on both peninsular Malaysia (4.1–4.9 animals/ha in primary lowland forest; Harrison 1969; and 11.5 animals/ha on Kedah Peak; Langham 1983), and on Borneo (16.6 animals/ha in logged-over forest; Steubing & Gasis 1989). An estimate of 23 animals/ha (Happold & Happold 1992) in montane grassland in Malawi was similar to that on Mt. Isarog and to estimates for *Proechimys semispinosus* on tiny islands in Panama (Adler in press and Adler *et al.*, in press).

The mean biomass of non-volant small mammals in the mossy forest on Mt. Isarog was estimated to be 1,554.9 g/ha. This is about twice the estimated biomass of non-volant small mammals in primary and secondary forest in peninsular Malaysia (730–840 g/ha) and three times the biomass of rodents only (400–525 g/ha) in the same habitat and area (Harrison 1969). Our figure also exceeds the estimate of 614 g/ha biomass of non-volant small mammals in montane grassland at 1900 m in Malawi (Happold & Happold 1992). Rodents in most communities in the dry and moist tropical forests on the mainland in Panama have much higher biomass, 4025 g/ha and 6304 g/ha, respectively (Fleming 1975) due to the presence of the large-bodied caviomorphs (agoutis and pacas), but Adler (in press) documented biomass values of 4380–17068 g/ha for a single species of echimyid (*Proechimys semispinosus*) on the tiny islands in Lake Gatun referred to above.

The estimates of density and biomass of non-volant small mammals on Mt. Isarog presented here are the first available data for a small mammal community in the mossy forest anywhere in the Philippines or Southeast Asia. The causes of their very high density and biomass, compared with the small mammals in the lowlands of Malaysia and Sabah, invite further investigation of these parameters in small mammals at high elevation habitats in the tropics. The apparent numerical dominance of a few species in this community is contrary to the prediction by MacArthur (1969) of a lack of numerical dominance in tropical communities. *A. musculus* was the most abundant species, and it, together with *R. everetti*, comprised 76% of the community. Evidence from previous studies also suggested that numerical dominance by two or three species appears to be common in tropical small mammal communities (e.g., Fleming 1975, O'Connell 1979, Fa *et al.* 1990).

Home range and movement. Data on home ranges of small mammals in tropical forest are quite limited, especially from montane forests. We found home ranges that were moderately large, with average estimates of nearly one-fourth hectare in a small mouse (*Apomys musculus*), and nearly half of a hectare in a large rat (*Rattus everetti*), with some individuals having ranges twice the average (Table 4). The high relative density for the community estimated from earlier studies (measured as number of individuals captured per 100 trap-nights; Rickart *et al.* 1991) had led us to expect small home ranges at the outset of the study, but this was not the case; we found home ranges to be large and overlapping, rather than small and non-overlapping.

The scansorial habits of some of the Philippine murids has been suggested in previous studies, as inferred from the long tails, structure of foot pads, etc. (Musser 1982, Musser & Heaney 1992) and has been observed in *A. musculus* and *R. everetti* on Mt. Isarog (Balete 1995). However, this vertical dimension in their spatial utilization was not reflected in the estimates of home ranges presented here. The measures given here, therefore, may not reflect the actual ecological relationships of these species; incorporating their above-ground movements in future studies would help to further refine the data presented here.

Mammals in Mossy Forest. The Philippine Islands support one of the highest levels of endemism among mammalian faunas. Many of those unique species occur in an equally unique environment, high elevation mossy forest. Temperature at the site is extremely stable, and there is no month when rainfall was less than c. 500 mm, leading one to imagine an environment that is stable overall. However, the site had exceptionally high estimated annual precipitation, about 12 meters, and nearly 2 meters of rain fell in a single month. Hence, we define the climate as cool and continuously moist with seasonal deluges.

This community of small mammals is not unusually species-rich, with only eight species known from the area, and six recorded on the trapping grids. However, the total density is quite high, one of the highest yet recorded in tropical rainforests. Associated with high density was moderately high biomass: only communities of tropical rodents on tiny islands or with very large-bodied species such as agoutis and pacas have higher estimated biomass. Contrary to some theoretical expectations, numerical dominance was present in estimates of density and biomass. Mean distances moved and estimates of home range size varied greatly among species, but were generally high. Our limited data indicate that individuals of any given species overlapped with many conspecifics, as well as with many non-conspecifics. In general, the image is one of an unusually dense population of rodents in which movements and overlap are great.

The virtual lack of comparable data elsewhere in mossy forest in the tropics does not permit us to know if these patterns of environment and population biology are directly related, nor to know if such conditions are common in other high-elevation tropical forest. Our observations elsewhere in the Philippines suggest that they are, but hard data are lacking. The unusual features of both the environment and the rodent community suggest that further investigations would be well worth the effort.

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