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**SMALL MAMMALS OF THE  
CAJAS PLATEAU, SOUTHERN ECUADOR:  
ECOLOGY AND NATURAL HISTORY**

**Adrian A. Barnett**

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# SMALL MAMMALS OF THE CAJAS PLATEAU, SOUTHERN ECUADOR: ECOLOGY AND NATURAL HISTORY

Adrian A. Barnett<sup>1</sup>

## ABSTRACT

We captured 483 small mammals (19 species: 1 insectivore, 2 marsupials, 16 rodents) from sites between 2700 and 4000 m on the Cajas Plateau, Azuay Province, Ecuador. Fifteen species were taken in montane forest and 10 on the páramo. Five species occurred in both habitats. One species was new to science, three were recorded for only the second time and three records were major range extensions, including one species new to Ecuador. Comparisons with other Andean sites show the species diversity of small mammals on the Cajas Plateau to be among the highest recorded in the Andes. Reasons for this are discussed. Data are presented on habitat preferences, reproduction, diet and pelage variation for each species. Litter sizes at the small end of a species' range were consistently observed. Adversity selection (*sensu* Southwood, 1977) at high altitude is suggested as an explanation. The natural history of several species is reported for the first time since their original discovery.

## RESUMEN

Se capturaron 483 pequeños mamíferos pertenecientes a 19 especies (1 insectívoro, 2 marsupiales y 16 roedores) desde sitios ubicados entre 2700 y 4000 m de altura en la Planicie de Cajas, Provincia de Azuay, Ecuador. Se capturaron 15 especies en la selva de montaña y 10 en el páramo. Cinco especies se encontraron en ambos hábitats. Una especie fue descrita como nueva para la ciencia, tres fueron registradas sólo por segunda vez y tres significaron extensiones de rango mayor, incluyendo una especie nueva para el Ecuador. La diversidad de especies de pequeños mamíferos de la Planicie de Cajas es una de las más altas registrada para los Andes, de acuerdo a una comparación con otras áreas. Se discuten las razones de este hallazgo. Se presenta información sobre preferencias de hábitat, reproducción, dieta y variación de pelaje de cada una de las especies. El tamaño de camada observado se situó consistentemente en el rango inferior de cada especie. Se sugiere como explicación a esto último la selección por adversidad (*sensu* Southwood, 1977) a latitudes altas. La historia natural de varias de las especies reportadas se describe por primera vez desde su descubrimiento original.

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## INTRODUCTION

Ecuador is one of the world's most biodiverse countries (Gentry, 1977; Mittermeier et al., 1997), with approximately 340 species of mammals (Barnett and Shapley, in prep. a)<sup>2</sup>. Despite this diversity, studies of Ecuador's mammals are few compared to other Neotropical countries. Recent work on the small mammals of Ecuador<sup>3</sup> has made substantial contributions and yet mammals under 1 kg still remain under-studied in Ecuador in comparison to neighboring countries. This is illustrated by data from the *Zoological Record*. From, 1981 to, 1996, while this organ gave the number of papers published on free-living native small mammals in Colombia as 35, 50 for Peru, and 77 for Venezuela, Ecuador was limited to 20 papers.

This paper is a summary of work conducted on the small mammals of Cajas region of Azuay Province, Ecuador. It was part of an Anglo-Ecuadorian research initiative that worked first in the páramo (1981-84) and then in the cloud forest vegetation of the region (1987-95) (see Barnett, 1986, 1988a; Barnett and Gretton, 1987). Mammal survey work was conducted between 1981 and 1987. For several of the species covered here these reports are the first to appear on their natural history since the species' original description.

Following these research periods, papers have been published on the bats (Robinson, 1989), birds (Barnett, 1988b; King, 1989), invertebrates (e.g., Read, 1986), and plants (Aguilar and Espinoza, 1990-1991; Flores, 1993; Ramsay, 1992; Ramsay and Oxley, 1996) of the Cajas region, and a number of papers on individual species of non-volant mammals have appeared (Barnett, 1985, 1987, 1991, 1992, 1997a, b; Jenkins and Barnett, 1997; Barnett and Muleon, 1999). These publications have not included all the non-volant small mammal species known to occur on the Plateau. This paper is an attempt to rectify this and to

<sup>2</sup>This is substantially more than the 271 reported by Groombridge (1992). A copy of the species list may be obtained by writing to the author.

<sup>3</sup>(e.g., Figueroa and Albuja, 1983; Voss, 1983; Patton, 1984; Orcés, 1986; Voss, 1988; Carleton and Musser, 1989; Albuja, 1991; Barnett, 1991; Best, 1991; Barnett, 1992; Parker and Carr, 1992; Voss, 1992; Ragout and Albuja, 1994; Suarez et al., 1995; Albuja and Patterson, 1996; Barnett, 1997a; Jenkins and Barnett, 1997; Schulenberg and Awbrey, 1997; Barnett and Muleon, 1999; Tirira, 1999).

present, in one place, comparative information on the habits and habitats of all the small mammal species known to occur on the Cajas Plateau. A fuller analysis of the biogeographic significance of Cajas will appear elsewhere (Barnett, in prep.). Unless otherwise stated, taxonomy follows Wilson and Reeder (1993).

### ACKNOWLEDGEMENTS

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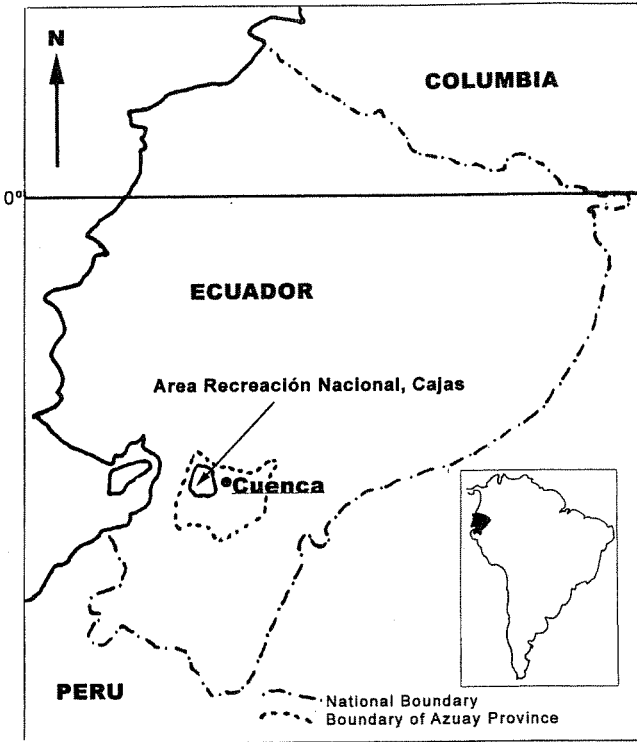
### SITE DESCRIPTIONS

The Cajas Plateau, a formerly glaciated 25 x 27 km<sup>2</sup> isolate of the Sierra de Machangara of the western Cordillera in the Ecuadorian Andes, lies some 25 km northwest from the town of Cuenca (2°52'S, 78°54'W) (see also Map 1). It is represented on 1:50,000 maps CT-NV-3785-I, II, III and IV and CT-NVI-BI-3784-IV, Instituto Geographico Militar, Quito. The plateau has a mean altitude of 3700 m, with peaks to 4138 m (Mt. Soldados). Colinvaux et al. (1997) give a detailed vegetational history of the Cajas area for the last 13,000 years, based on palynological analysis of cores from Lake Llaviuco. Our surveys included cloud forest<sup>4</sup> and páramo vegetation types.

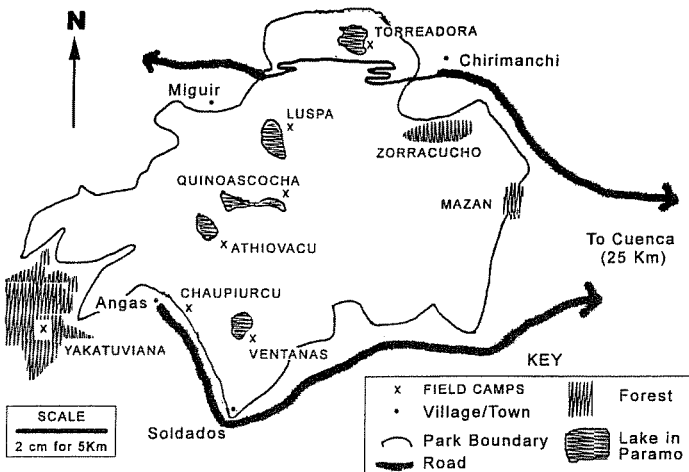
On the Cajas Plateau the treeline is at  $\approx$  3400 m. Below this there are several forest types. Areas of primary cloud forest are found in the Rio Mazán valley (see Fig. 1). These were dominated by *Ocotea* aff. *nectandra* (Lauraceae), *Podocarpus* sp. (Podocarpaceae), *Clusia* spp. (Clusiaceae), and *Weinmannia fagaroides* (Cunoniaceae), interspersed with small areas of secondary forest dominated by

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<sup>4</sup> *sensu* Patterson et al. (1998).



Map 1: Location of Area Recreación Nacional Cajas in Ecuador.



Map 2: Sketch map of Area Recreación Nacional Cajas, showing study sites.



Figure 1. Primary cloud forest of the Rio Mazan valley (altitude 500-2800 m), showing one of the valleys many waterfalls. Photograph, Adrian Barnett.

species of *Miconia* (Melastomataceae), including *M. crocea*. In the Zorracucho Valley the slopes were covered with *Myrtus*-dominated secondary forest interspersed by breaks of bamboo (mostly *Chusquea* spp.) and planted stands of *Pinus* and *Eucalyptus* and an open valley floor covered with prominent clumps of the graze-resistant shrub *Barnadesia* aff. *arborea* (Asteraceae). Both the Mazán and Zorracucho valleys are on the eastern-facing side of the plateau. A third site, Yakatuviana, was on the western-facing slope and was much moister than the other two. Lamentably, the study site was highly disturbed, the formerly extensive *Clusia*-dominated forest having been largely replaced with breaks of *Chusquea* bamboo. Detailed botanical descriptions of specific localities are provided by Fleming (1986) and Jacques et al. (1986), while Grubb et al. (1977), Patzelt (1986), and Sarmiento (1987) provided general and photographically illustrated descriptions of Ecuadorian cloud forest structure and composition. Floristically, the forests on the western side of the Cajas Plateau are similar to those at Pasachoa described by Jørgensen and Valencia (1988) and those to the south described by Madsen and Ollgaard (1994). Because they face the Pacific Ocean, the forests on the western slope of the Andes (e.g., at Yakatuviana) are much moister and warmer than their eastern counterparts (see Grubb, 1977; Patzelt, 1986; Sarmiento, 1987).

Between the forest and the páramo, at  $\approx 3500$  m, is a shrubby ecotone some 100 m wide. Above this is páramo moorland (see Fig. 2), corresponding to the 'grassy páramo' division of Cuatrecasas (1968) and Harling (1979). Within this there are three broad subdivisions; *pajonal* (grass páramo) from 3400 m to 4000 m and, above this, shrub and cushion páramo (= *yareta*)<sup>5</sup>. The third division, *quenoa* forest, occurs in sheltered locations in both páramo belts (see Fig. 2). Pajonal and yareta are both mosaics of vegetation types, whose local composition is influenced by drainage and exposure (Smith, 1977; Van Der Hammen and Cleef, 1986).

In pajonal several different micro-environments are found. At any altitude the most exposed areas are dominated by plants with low-growing and cushion-like growth forms (see Acosta-Solis, 1966; Van Cleef, 1981). In sheltered areas there are *quenoa* forests dominated by the short, twisted trunks of *Polylepis* (Roseaceae) trees (see Fig. 3). The edges of the forests frequently have dense stands of composite shrubs (*Gynoxis* and *Diphlostephium*) that act as windbreaks. These near windless, moist environments have a dense cover of ground-living and epiphytic bryophytes. Along with gullies ('*quebradas*'), rock outcrops and riverbanks, these forests form mesic islands in an otherwise wind-dried environment (see Simpson, 1979a; Barnett, 1992; Ramsay, 1992; Ashe and Leschen, 1995; Fjeldsá and Kessler, 1996). In the *quebradas* there is less moss cover and characteristic vegetation includes *Bomarea* vines (Alstroemeriaceae) and shrubs of the genera *Cavendishia* (Ericaceae), *Baccharis* (Asteraceae) and

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<sup>5</sup> though this is a common name of a páramo plant (*Azorella*) in the altiplano of Peru, Ramsay (1992) has used it to describe the community of cushion plants of which *Azorella* is characteristic, a use that is followed here.



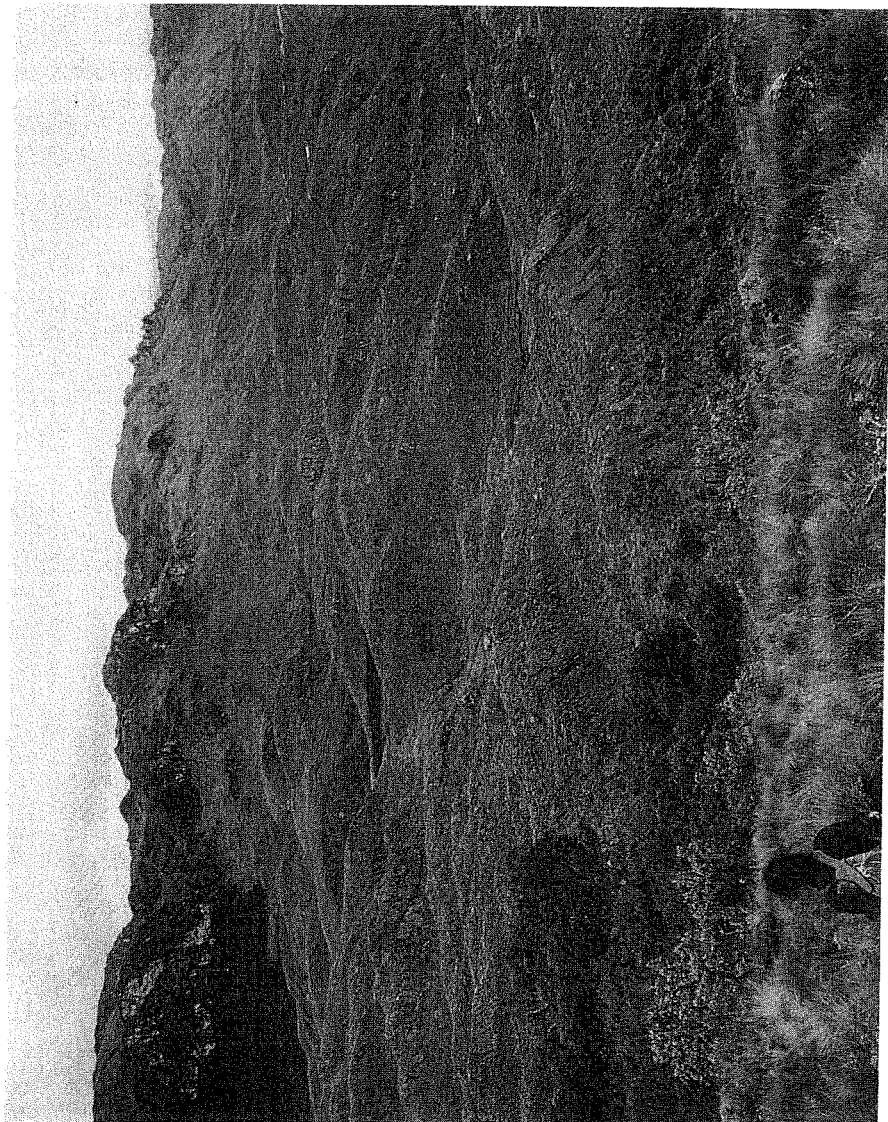


Figure 2. Páramo showing pajonal grassland and quenoa forests. Note the small extent of the forests and their restriction to sheltered areas. Near Lake Torreadora (4000 m). Photograph, Adrian Barnett.



Figure 3. Interior of a quenoa forest, showing tangled nature of the *Polylepis* trees, the low canopy and the thick mossy groundcover (near Lake Torreadora, 4000 m). Photograph, Adrian Barnett.

*Calceolaria* (Scrophulariaceae). Rock outcrops (see Fig. 4) frequently shelter *Calceolaria* spp. and members of the ericaceous genera *Maclenia*, *Gautheria* and *Pernettya*.

The páramo of Cajas has been quantitatively analyzed by Ramsay (1992), who distinguished six vegetation associations. A botanical summary of those relevant here are presented in Table 1.

Around 80% of the Cajas Plateau lies within the boundaries of the Area Nacional de Recreacion, Cajas (ARN) (see Huber, 1979). As such it has received some wardening and protection since the ARN's inception in 1976. Nevertheless, some parts of the ARN are subject to intense human pressure, including cattle grazing and deliberate fire-setting as part of local range-management practices (Huber, 1979; Ramsay and Oxley, 1996; see also Knapp, 1991). Other areas are popular with fishermen and few areas remain fully undisturbed (Barnett, 1997a, b).

As with páramos elsewhere (Ralph, 1978; Smith, 1972; Baruch, 1979; Smith, 1981; Van Der Hammen and Cleef, 1986), exposure and wind chill can be important physical constraints on the fauna and flora of Cajas. There is no permanent snowline, though snow may fall on the higher peaks at any time of year. Weather is frequently cold and overcast and winds often gust to over 60 kmph (see Ramsay, 1992; Barnett, pers. obs.). Daily temperature ranges from  $-6^{\circ}\text{C}$  at night to  $27^{\circ}\text{C}$  during the day. This exceeds the annual mean temperature variation. There has been no long term collection of meteorological data on Cajas, but 30 years of records for Cuenca (2000 m) show that rainfall is highest between March and May. The dry season is from June to January in southern Ecuador (Ramsay, 1992), with the lowest rainfall in Cuenca between June and September (Meteorological Office, 1977).

## METHODS

Prior to the fieldwork covered in this report, the small mammals of the Cajas Plateau were effectively unstudied (see Huber, 1979). The main aim, therefore, was to obtain the most representatively accurate sample of the species present over the whole plateau, rather than conduct detailed quantitative investigations of particular areas within the ARN. This influenced the operational regime deployed. Study sites were chosen to cover the full range of habitat types in the ARN and adjacent areas. Eleven sites were visited (see Map 2). Information on the altitude and habitat types of these is given in Table 2. The rugged terrain made the use of regular trapping grids ineffective. Accordingly, traps were placed at runs, holes, and other sites of small mammal activity (see Twigg, 1975a; Gurnell and Flowerdew, 1990; Barnett and Dutton, 1995). This provided less quantifiable results but probably increased trapping success, an acceptable compromise in little-known areas (Barnett and Dutton, 1995; Barnett, 1996; Stork and Davies, 1996). A mixture of traps were used, including live (Longworths, Shermans, and Havaharts) and snap traps



Figure 4. A rock outcrop with attendant *Calceolaria* shrubs. Near Lake Luspa (3700 m). Photograph, Adrian Barnett.

Table 1. Summary of the botanical characteristics of paramo-sub-types at Cajás (modified from Ramsay, 1992).

Name of paramo sub-type	Altitudinal range	Floral characteristics
<i>Viola humboldtii</i> pajonal	3500-3600 m	Dominated by <i>Calamagrostis</i> bunchgrass with scattered shrubs and low-growing rosette plants including <i>Viola humboldtii</i> , <i>Azorella pedunculata</i> , <i>Halenia weddelliana</i> , <i>Geranium reptans</i> , <i>G. multipartium</i> and <i>G. sibbaldoides</i> .
<i>Paspalum</i> pajonal	3500-3600 m	More open grassland than <i>V. humboldtii</i> -grassland with a higher proportion of <i>Paspalum tuberosum</i> (Graminae), mixed with <i>Lycopodium clavatum</i> (Bryophyta: Lycopodiaceae), <i>Eryngium humile</i> (Asteraceae), <i>Hypochaeris sessiliflora</i> (Asteraceae) and <i>Hypericum</i> (Guttiferaceae).
Shrubby páramo	3800 m	Characterized by composite shrubs of the genus <i>Baccharis</i> (inc. <i>B. alpinum</i> ), <i>Diphlostephium</i> (inc. <i>D. hartwegii</i> ) and <i>Chusquiragua insignis</i> , and the herbs <i>Gentiana diffusa</i> (Gentianaceae), <i>Baccharis genistelloides</i> and <i>Castilleja pumila</i> (Scrophulariaceae).
Yareta Cushion páramo	3800 m	Dominated by plants with low-growing and cushion-like growth forms, of which <i>Hypochaeris sessiliflora</i> and <i>Werneria nubigena</i> (Asteraceae), <i>Phyllactis rigida</i> (Valerianaceae), the gentians <i>Gentiana sedifolia</i> and <i>Halenia mayeri</i> and <i>Isöetes andina</i> (Pteridophyta: Isoetaceae) are characteristic. <i>Azorella compacta</i> (Umbelliferae) is also present.

(Nippers, Little Nippers, Self-sets, and locally available metal snap-traps of Chinese manufacture)<sup>6</sup>.

Traps were flagged to aid re-location and staked and tied to avoid removal by scavengers (see Gurnell and Flowerdew, 1990; Barnett and Dutton, 1995). In especially dense and difficult terrain, where the visual horizon was less than the distance between the traps (notably in quenoa forests and cloud forest), a white cord was run between traps at eye height (termed 'festooning' by Barnett and Dutton, 1995) to speed trap location and so minimize vegetation damage and

<sup>6</sup> Manufacturers' information:

Havahart traps, Havahart Ltd., Box 551, Ossining, New York, USA;

Longworth Live traps, Penlon Ltd., Radley Road, Abingdon, Oxfordshire, OX14 3PH, UK;

Sherman traps, H.B. Sherman Inc., P.O. Box 20267, Tallahassee, FLA 32316, USA;

Nippers and Little Nippers, Procter Bros. Ltd., Pantglas Industrial Estate, Bedwas, Newport, Gwent NP1 8XD, UK;

Self-sets, Falcon Works, Hanworth Road, Sunbury-on-Thames, Surrey, TW16 5DE, UK.

Table 2. Site descriptions.

Locality	Altitude	Description
Lake Torreadora	4000 m	Area of <i>Viola</i> pajonal with frequent quenoa forests and some areas of marshland <i>Paspalum</i> pajonal and yareta. Forests and grassland subject to heavy visitor pressure. Frequent waterfalls and streams.
Athiovacu	3900 m	Small, steep-sided protected valley filled with shrubby páramo and quenoa forest. Little disturbance.
Lake Quinoascocha	3800 m	Very exposed locality. <i>Viola</i> pajonal, quenoa forest, <i>Gynoxis</i> clumps and scrub-dotted scree. Little disturbance.
Chapiurcu	3750 m	Wide shallow valley filled with remnants of once-considerable quenoa forest, now greatly fragmented by herding activities and woodcutting.
Lake Luspa	3700 m	<i>Viola</i> pajonal, <i>yareta</i> , marsh and quenoa forest. Disturbance by grazing, recreational fishing, and tourism.
Ventanas	3650 m	Heavily grazed grassland, formerly <i>Viola</i> and <i>Yareta</i> , but with close-cropped grass tussocks all most rosette plants trampled. Some quenoa forest and rock outcrops.
Chirimanchi	3450 m	Stunted trees and shrubs at páramo/montane forest ecotone.
Lake Llaviuco (Zorracucho valley)	3100 m. (eastern side of plateau)	Secondary montane forest on valley sides. Grazed valley floor. Reedy marsh around lake.
Rio Mazán valley	2700 m (eastern side of plateau)	Primary <i>Podocarpus</i> and <i>Ocotea</i> -dominated montane forest, with some secondary forest and areas of grazed grassland.
Yakatuviana	2400 m (western side of plateau)	Bamboo ( <i>Chusquea</i> spp.)-dominated montane forest. Some small-scale agriculture.

associated reduction of trap success. Bait was a mixture of porridge oats, cooking oil, banana and water. Sardines, tuna, trout flesh, sausage, or meat were used for faunivorous species. Snap-traps were checked twice a day from 0700 to 0800 hrs and from 1200 to 1300 hrs. Live-traps were checked from 0600 to 0700 hrs and from 1700 to 1800 hrs. Data collection methods and specimen preparation followed Corbet (1968). Methodology for capture-mark-release studies followed Twigg (1975b). Field work took place between June and October in 1981, 1983, 1984, 1986, and 1987.

All specimens were initially identified by Martin C. Perry of the Mammal Section, Natural History Museum, London. Specimens of *Microryzomys* were subsequently re-identified by Michael Carleton and Guy Musser (see Carleton and Musser, 1989), and some specimens of *Oryzomys* were subsequently re-identified by Guy Musser (AMNH), while Rob Voss (AMNH) re-identified some specimens of *Thomasomys*. Synonymies for all species collected are given in Appendix 1. Unless there is a more recent taxonomic treatment, these are based on Wilson and Reeder (1993).

## RESULTS

**General trapping.**—The total trapping effort was 5942 trap nights. This consisted of 4178 trap nights in páramo and 1764 trap nights in cloud, pine, and *Eucalyptus* forests (1302 at Mazán, 402 at Llaviuco, 60 at Yakatuviana). Of these 1666 trap nights were expended live-trapping for fishing mice (Ichthyomyini), 130 were spent live-trapping at Llaviuco and a further 240 spent studying movement patterns of rodents inhabiting quenoa forest.

Four hundred and eighty three individual small mammals were captured. Of these 468 were rodents (16 species, 8 genera), twelve were insectivores (1 species) and three were marsupials (2 species, 1 genus). Of these 440 were made into museum specimens. In addition, 53 examples of non-target species were also caught; rufous ant-pitta *Grallaria rufula* (3), plumbaceous sierra finch *Phrygilus unicolor* (1), bar-winged cinclodes *Cinclodes fuscus* (6), frogs of the genera *Atelopus*, *Eleutherodactylus*, and *Gastrotheca* (17), and invertebrates (mainly gastropods, phasmids, and coleoptera, 26). Unlike lowland sites (Barnett and da Cunha, 1994), bait removal by ants at Cajas was minimal (less than 1% of trap-nights), but 8% of trap-nights were lost to rain disturbance (traps set off or bait washed off). One site was subject to disturbance by large mammals.

**General snap-trapping.**—In 3906 trap nights, 229 specimens of 18 species were caught. The low overall trap success (5.86%) masks great inter-site and inter-habitat variability in trapping success (see Table 3)<sup>7</sup>.

**Trapping for fishing mice.**—Three specimens of one ichthyomyine species, *Chibchanomys orcesi*, were captured in live traps. In addition, three shrews,

<sup>7</sup>data is given for all sites except Athiovacu, for which trapping data has been lost.

Table 3. Snap-trap success and small mammal community composition between localities and habitats.

Locality, Habitats.	% Trap success	% <i>Akodon mollis</i>	Species captured
<u>Lake Torreadora</u>	68.6	77.3	
Quenoa	11.1	54.6	<i>C. montivaga</i> (quenoa, quebradas)
<i>Viola</i> pajonal	07.0	85.7	<i>A. mollis</i> (all, except bog)
<i>Paspalum</i> pajonal	12.12	75.0	<i>M. altissimus</i> (quenoa, rock outcrops)
Rock outcrops	12.7	62.5	<i>P. haggardi</i> (rocks, paspalum)
Quebradas (gullies, streamsides)	10.5	62.7	<i>T. gracilis</i> (quenoa)
Shrub patches			<i>T. pyrrhonotus</i> (quenoa)
Quaking bog			<i>S. inopinatus</i> (quaking bog)
House			
<u>Athiovacu</u>			
Quenoa			no information
<i>Viola</i> Pajonal			
<u>Lake Quinoascocha</u>	07.1	73.9	
<i>Paspalum</i> pajonal	09.33	100	<i>C. montivaga</i> (quenoa)
Shrub patches	06.3	80.0	<i>A. mollis</i> (all)
Quenoa	06.9	41.7	<i>M. altissimus</i> (quenoa, paspalum pajonal)
			<i>T. cinnameus</i> (quenoa, shrub patches)
			<i>T. gracilis</i> (quenoa)
<u>Chapiurcu</u>	12.7	73.33	
Quenoa	12.4	100	<i>C. montivaga</i> (quenoa)
Shrubs	10.1	80.0	<i>A. mollis</i> (quenoa, shrubs)
Riverbank	20.0	40.0	<i>M. altissimus</i> (quenoa, streamsides)
			<i>P. haggardi</i> (rocks)
			<i>S. inopinatus</i> (riverbank quebrada)
			<i>T. gracilis</i> (quenoa)
<u>Lake Luspa</u>	22.3	55.5	
Quenoa	19.4	32.0	<i>C. montivaga</i> (quenoa, quebradas)
<i>Viola</i> pajonal	26.0	50.0	<i>A. mollis</i> (all, except stream)
<i>Paspalum</i> pajonal	08.7	50.0	<i>C. orcesi</i> (stream)
Rock outcrops	75.0	44.5	<i>M. altissimus</i> (quenoa, rocks)
Quebradas	19.0	38.5	<i>P. andium</i> (rocks)
Shrub patches	14.8	100	<i>T. gracilis</i> (quenoa, rocks)
			<i>T. pyrrhonotus</i> (quenoa)
<u>Ventanas</u>	13.75	47.6	
Quenoa	12.5	33.33	<i>A. mollis</i> (pajonal, quenoa)
<i>Viola</i> Pajonal	15.0	100	<i>M. altissimus</i> (quenoa)



<u>Chirimanchi</u> Streamside quebrada	15	50	<i>C. montivaga</i> <i>A. mollis</i> <i>M. altissimus</i>
<u>Lake Llaviuco</u> (Zorracucho valley) Secondary forest Marsh Grazed grassland Riverbank <i>Eucalyptus</i> grove	11.2 09.2 02.5 02.5 05.0 01.7	26.46 0 33.0 100 0 100	<i>A. mollis</i> (marsh, grassland, <i>Eucalyptus</i> / <i>Pinus</i> ) <i>A. orophilus</i> (forest) <i>C. orcesi</i> (streams) <i>M. altissimus</i> (forest) <i>M. minutus</i> (forest) <i>O. destructor</i> (forest, hut, streambanks) <i>T. aureus</i> (forest, marsh) <i>T. baeops</i> (forest) <i>T. gracilis</i> (forest, marsh) <i>T. paramorum</i> <i>T. pyrrhonotus</i> (forest)
<u>Rio Mazán valley</u> Podocarpus forest Riverside Grazed grassland	7.0 5.6 6.9 9.6	51.4 0 56.1 75.0	<i>C. caniventer</i> (forest) <i>C. tatei</i> (forest) <i>C. montivaga</i> (forest) <i>A. mollis</i> (grassland) <i>A. orophilus</i> (forest) <i>O. albigularis</i> (forest) <i>T. aureus</i> (forest) <i>T. baeops</i> (forest) <i>T. paramorum</i> (forest)
<u>Yakutuviana</u> Primary forest Secondary forest Agricultural field	11.1 02.5 09.7 12.5	64.3 0 28.6 100	<i>A. orophilus</i> (secondary forest, field) <i>O. albigularis</i> (primary and secondary forest) <i>T. paramorum</i> (secondary forest)

*Cryptotis montivaga*, and 232 individuals of 6 rodent species (200 *A. mollis*, 4 *Microrzomys altissimus*, 1 *Oligoryzomys destructor*, 8 *Oryzomys albigularis*, 1 *Sigmodon inopinatus*, 8 *Thomasomys gracilis*) were caught in 1666 trap nights (see Barnett, 1997a: table 1). Fourteen non-mammals were also captured. While total mammal trap success was 14.28%, trapping success for ichthyomyiines was very low (0.21%).

**Movement patterns of quenoa-forest inhabiting rodents.**—Four lines of twelve Longworth live traps were set for five nights, with equal proportions of traps in the quenoa and adjacent grassland. Inter-trap distance was  $\approx 10$  m, transects were  $\approx 100$  m apart. Twelve individuals from four species (*Akodon mollis*, *Microrzomys altissimus*, *Thomasomys cinnameus*, *Thomasomys gracilis*) were caught a total of 36 times in 240 trap nights. The results of the capture-mark-

Table 4. Live-trapping data showing distances traveled and percentage occupancy of dense cover.

Animals captured	Number of Recaptures	Distance (m) between Recaptures <sup>1,2</sup>	Maximum inter-trap Distance <sup>3</sup> (m)	% records in Dense cover <sup>4</sup>
<i>A. mollis</i> 1	2	138, 0	138	100
<i>A. mollis</i> 2	4	40; 110; 34, 0	110	50
<i>A. mollis</i> 3	4	112, 0; 0; 41.6	112	25
<i>A. mollis</i> 4	0	-	-	0
<i>M. altissimus</i> 1	0	-	-	100
<i>M. altissimus</i> 2	3	0; 20; 31.2	31.2	33.3
<i>T. cinnameus</i> 1	2	0; 10	10	100
<i>T. cinnameus</i> 2	3	11.5, 0; 0	11.5	100
<i>T. gracilis</i> 1	1	152.3	152.3	100
<i>T. gracilis</i> 2	0	-	-	100
<i>T. gracilis</i> 3	1	10	10	100
<i>T. gracilis</i> 4	4	10; 0; 20; 11.7	20	100

1: 0 indicates caught in the same trap as proceeding record.

2: calculated by direct line measurement between traps.

3: includes all habitat types, value = direct line measurement.

4: calculated by number of records in each habitat type.

recapture study are given in Table 4 and discussed on a species-by-species basis under the species headings.

**Trapping in Pine Plantations and in *Eucalyptus* plantations and live-trapping, Zorracucho valley.**—Sixty nights snap-trapping in pine and *Eucalyptus* plantations near Lake Llaviuco yielded a single immature male *Akodon mollis*. The open, grazed floor of the valley was regularly disturbed by cows and children. Live-trapping there with Longworths for 130 nights caught three *A. mollis*.

## DISCUSSION

**Trapping.**—Capture rates in Cajas were much higher than those generally expected of the species-rich, numbers poor tropical lowland communities, where rates of 0.5-2.5% are common (Voss and Emmons 1996)<sup>8</sup>. Similar success rates to those in Cajas have been reported in other Andean communities (e.g., Meserve et al., 1982; Murúa and González, 1982; Meserve et al., 1991). Such low trapping rates as have been reported for Andean small mammal communities (e.g., Zuniña et al., 1983, 0.33% and 0.43%; Péfaur and Díaz-de-Páscual, 1985, 3.75%; Lopez-Arevalo et al., 1993, 4.31%; Durant and Díaz, 1995, approx. 2.68%) are most

<sup>8</sup> though this pattern is not universal. Studies by James Patton in western Brazil obtained trap success between 5 and 12% in terra firme forest, and even higher in várzea, though these numbers varied seasonally (J. Patton, pers. comm., 1998; Patton et al., 1994).

probably methodological artifacts resulting from the use of brief sampling periods (Zuniña et al., 1983; Péfaur and Díaz-de-Páscual, 1985), the exclusive use of live-traps (e.g., Lopez-Arevalo et al, 1993, which generally give a lower capture success rate than snap traps [see Hansson and Hoffmeyer, 1973; Barnett and Dutton, 1995]), or both (Durant and Díaz, 1995). A number of authors (e.g., Emmons, 1984; Barnett and da Cunha, 1994; Voss and Emmons, 1996; Barnett and da Cunha, 1998a) have reported positive correlations between trapping success and soil fertility. Accordingly, the high trap success at Cajas (and elsewhere in the moist Andes) may be attributable to the fertile volcanic-derived soil of much of the mountain chain (see Kennerley, 1980; Owen, 1990).

Trap success was highest in quenoa forest and in rock falls. It is unclear if this is because there were more animals there, or because the physical structure of the habitat assisted entrapment (moss-covered floors easily reveal small mammal trails—see Carey and Witt, 1991; Malcolm, 1991) and rock jumbles limit the places for a small mammal to run (Barnett and Dutton, 1995). The low capture rates in pine and *Eucalyptus* plantations are in line with data from similar plantations in other countries (e.g., Friend, 1982; Happold and Happold, 1987; Mitchell et al., 1995; Stanko et al., 1996; Zejda and Nesvadbova, 1996) and may be due to the poorly developed groundcover and leaf litter layers and the dearth of insect and seed forage available (see Allen et al., 1995; Ogden et al., 1997).

The low capture rates for ichthyomyines was not unexpected as trap-shyness seems to be typical for the group. As examples, Anthony (1921: 2) reported that having obtained the type of *Ichthyomys tweedi*, "although traps were set out in every suitable locality ... no additional specimens were secured" (see also Anthony, 1929: 1); Andrea Pogson and Caroline Lees trapped specifically for ichthyomyines and caught one in 700 trap nights (see Barnett, 1997a), and Ochoa and Soriano (1991) reported very low success trapping for *Neusticomys mussoi* in Venezuela, as did Durant and Díaz (1995) for *Ichthyomys hydrobates*.

Live trapping results from the quenoa forest and páramo showed that, of the 12 animals caught, only four were trapped away from dense cover. *A. mollis* showed the greatest mobility, with a mean maximum inter-trap distance (m.m.i.d.) of 120 m over the study period (see Table 4). *Thomasomys gracilis* was also quite mobile, with an m.m.i.d. of 45.5 m. *T. cinnameus* appeared to move little (m.m.i.d. of 10.75 m). These singularities may reflect differences in diet and the dispersion and patchiness of food resources, which has often been shown to influence the ranging patterns of small mammals (e.g., Dalby, 1975; Delany, 1986; R.G. Anthony et al., 1987; Happold and Happold, 1989, 1992; Canova and Fasola, 1993; Ellis et al., 1997). If this is occurring with *Akodon* and *Thomasomys* in the quenoa forests of Cajas, it is doing so counter-intuitively, for *Akodon* is a generalist (browse, fungi, seeds, and insects), while *Thomasomys* is predominantly frugivorous (see Nowak, 1991; Lopez-Arevalo et al., 1993). This would lead one to predict the reverse pattern of range sizes for the two genera. Larger sample sizes and quantified records of prey-base abundance and distribution are required before valid conclusions can be drawn.

### General Ecological Structuring

It is instructive to compare the number of species present at Cajas with those reported by other workers from other areas in the Andes. Comparisons are often difficult because of methodological differences<sup>9</sup>, which can lead to differences in the proportion of the catch each species represents (see Nichols, 1986). Comparisons are therefore restricted simply to the number of species, rather than any more refined standard of comparison.

The small mammal species diversity of the cloud forest zone of Cajas (2 marsupials, 1 insectivore, 12 rodents) compares favorably with similar high altitude forest study sites in Venezuela (Díaz-de-Páscual, 1984, 1994; Péfaur and Díaz-de-Páscual, 1985; Durant and Díaz, 1995), Colombia (Durant and Péfaur, 1984; Lopez-Arevalo et al., 1993), Ecuador (Albuja and Luna, 1997), and Peru (Dorst, 1958; Patton, 1986; Pacheco et al., 1993) and with the more xeric Peruvian communities Pearson (1951) and Pearson and Ralph (1978) studied (see Table 5).

However, the diversity of small mammals in the páramo of Cajas (1 insectivore, 9 rodents) is considerably higher than other comparable sites (Dorst, 1958; Durant and Péfaur, 1984; Lopez-Arevalo et al., 1993; Durant and Díaz, 1995), and close to that reported by Pearson (1951) and Pearson and Ralph (1978) (see Table 5). With the exception of Patton (1986) and Pacheco et al. (1993), the combined small mammal species diversity for montane forest and páramo is higher in Cajas than other studied sites (see Table 5). This may be due to the special biogeographical position of Cajas, which embraces the northern-most ingress of the genus *Phyllotis* and the southern-most extensions of the genera *Sigmodon* and *Cryptotis*.<sup>10</sup>

Comparison with Cotgreave's and Stockley's (1994) compilation of species diversity data for 25 small mammal communities around the world shows that Cajas is highly diverse. Only two of their listed sites had numbers of species comparable to Cajas<sup>11</sup>. However, Cajas' small mammal species diversity is between 105% and 51% of that collated by Voss and Emmons (1996) for 10 lowland rainforest sites in the Amazon Basin. The numbers of rodent species are broadly similar (range 11-27), and the differences are largely due to the absence of

<sup>9</sup> e.g., see Neal and Cock (1969), Schwan (1986) for trap type; Willan (1986) for bait; Hansson (1975) for quadrat size; Vickery and Bider (1981) for weather; Gurnell and Langbein (1983) for trap positioning; Tew (1987); Reynolds and Gorman (1994) for seasons and Shore and Yalden (1991), Tew et al. (1994) for minute variations in technique

<sup>10</sup> Formerly considered to occur no further south than Loja Province, Ecuador (see Barnett, 1992), *Cryptotis* has now been recorded in northern Peru by Vivar et al. (1997). *Sigmodon* is much more speciose in the northern part of its range (Voss, 1992). Cajas is the southern-most extension of *S. inopinatus* (Voss, 1992), with only *Sigmodon peruanus* from northern Peru occurring further south (Pacheco et al., 1995).

<sup>11</sup> though the scales are probably different. Though area is not always given, none of the sites used either by Cotgreave and Stockley or by Voss and Emmons would appear to cover an area comparable to Cajas' 25x27 km<sup>2</sup>.

Table 5. Comparative species diversity for Andean small mammal communities.

Study and habitat type	Location (situation, country, altitude).	Number of species (M=marsupials, I=insectivores, R=rodents)
<u>Montane forest</u>		
Díaz-de-Páscual, 1984	north-eastern Venezuela, 500 m	0 M, 0 I, 8 R
Durant and Díaz, 1995	north-western Venezuela, 1890-2600 m	0 M, 1 I, 9 R
Péfaur and Díaz-de-Páscual, 1985	north-eastern Venezuela, 1000-2500 m	16 and 17 species
Durant and Péfaur, 1984	Merida, Colombia, 1640-2500 m	1 M, 1 I, 5 R
Lopez-Arevalo et al., 1993	Cord. Oriental, Colombia, 2380-2900 m	2 M, 1 I, 5 R
Zuñinga et al., 1983	Cord. Occidental, Colombia, 2000-3000 m	1 M, 0 I, 2 R
this study	Cajas, Ecuador, 2400-3100 m	2 m, 1 I, 12 R
Albuja and Luna, 1997	Cord. de Cóndor, Ecuador, 1000-1600 m	1 M, 0 I, 3 R
Patton, 1986	southern Peru, 2000-3000 m	1 M, --, 10 R
Pacheco et al., 1993	central Peru, 1100-1880 m	3 M, --, 9 R
<u>High-altitude grassland</u>		
Durant and Díaz, 1995	north-western Venezuela, 3000-3950 m	0 M, 1 I, 3 R
Durant and Péfaur, 1984	Merida, Colombia, 3300-3600 m	0 M, 1 I, 3 R
Lopez-Arevalo et al., 1993	Cord. Oriental, Colombia, 3000-3380 m	0 M, 1 I, 4 R
this study	Cajas, Ecuador, 3300-4000 m	0 M, 1 I, 10 R
Dorst, 1958	Andes, central Peru ( <i>altiplano</i> ), 4000 m	0 M, 0 I, 8 R
Patton, 1986	Andes, southern Peru ( <i>puna</i> ), 3500-5000 m	---, ---, 13 R
Pearson, 1951	<i>Altiplano</i> , southern Peru, 3000-5000 m	5-14 R per site
Pearson and Ralph, 1978	Pacific-facing slope, northern Peru ( <i>puna</i> ), 3500-4500 m	1 M, 0 I, 16 R
Pacheco et al, 1993	Amazon-facing slope, central Peru, 2800-3450 m	1 M, --, 8 R

marsupials at higher altitudes compared to those in the Amazon (where there are between 5 and 12 marsupial species per site)<sup>12</sup>.

In Cajas, small mammal species diversity was slightly higher in the cloud forests than in the páramo (15 vs. 10 species), with 9 and 4 species, respectively being unique to each zone. The greater species numbers in cloud forest are probably a consequence of within-habitat variation attributable to the greater

<sup>12</sup> see also Pacheco et al. (1993).

variety of habitat types present at each locality (see Veillon, 1965; Pearson and Ralph, 1978; Gibb, 1981). It should also be noted that there is considerable between-site variation, with the three cloud forest areas sampled being very different in their dominant plant communities; Mazán was almost exclusively primary forest, Zorracucho was mostly secondary forest and Yakatuviana was much moister than either due to its location (the Plateau's Pacific-facing slope). This diversity may well have increased the pool of small mammal species available for sampling.

Above 2400 m, there are well-marked differences in plant communities that comprise the páramo grassland sub-types (see above and Table 1). However, the greatest number of small mammals was caught in sheltered areas (284 of 301 animals). Only four species (*Akodon mollis*, *Microryzomys altissimus*, *Phyllotis andium* and *P. haggardi*) were caught in grassland páramo and only the latter two were caught uniquely there. No animals were caught on *yareta* páramo. *Yareta* is highly exposed, lacks cover, and the surface, provided by the continuous cover of rosette plants, is hard and unyielding. This may have made it unattractive to small mammals. It would seem that the higher-altitude living rodents of Cajas favor habitats provided by quenoa forests, vegetated quebradas, and streamside vegetation. These probably provide both more shelter and more insect prey, significant factors when the diet so many high-altitude rodents includes insects (see Glanz, 1982; Lopez-Arevalo et al., 1993; Cotgreave and Stockley, 1994). Such habitats are both micro-geographically restricted and compositionally quite uniform (see Acosta-Solis, 1966; Simpson, 1976a; Ramsay, 1992), compared to montane forest (Veillon, 1965; Grubb, 1977; Grubb et al., 1977). Thus, from the small mammal perspective, the páramo may be less variable than it is to the eye of a botanist.

Higher species diversity at lower elevation is a common pattern for many taxa (see Rahbek, 1995) and has been documented in the montane small mammal faunas of Mexico (Fa et al., 1990), Peru (Pacheco et al., 1993), Malaysia (Medway, 1972), New Guinea (Laurie, 1952) and Africa (Misonne, 1963; Rowe-Rowe and Meester, 1982). However, this phenomenon is not uniform; the opposite trend having been observed in the western slope of the Peruvian Andes (Pearson and Ralph, 1978) eastern slope of the Peruvian Andes (Patton, 1986), on the eastern slope of the Venezuelan Andes (Péfaur and Díaz-de-Páscual, 1985), in the Ethiopian highlands (Yalden, 1988), and in Texas (Owen, 1990). Some studies (e.g., Heaney et al., 1982, in the Philippines; Happold and Happold, 1992, in Africa; Patterson et al., 1998, in Peru<sup>13</sup>) have found no difference in small mammal species diversity between altitudes, while others (e.g., Yu, 1994) have found greatest species diversity at intermediate altitudes. Intra-locality differences in

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<sup>13</sup> For a 3 km altitudinal transect from Amazon lowlands to the *Puna* grasslands of south-eastern Peru Patterson et al. (1998), found that the number of murid species showed little relationship to altitude. However, over the part of the altitudinal and habitat range comparable to the habitats present in Cajas, the number of all species of small mammal (marsupials and all rodents) was greater in montane forest than in high altitude grasslands (see data in Pacheco et al., 1993).

species diversity can have ecological and/or historical explanations (Endler, 1982; Vuilleumier and Monasterio, 1986; Voss and Emmons, 1996). Explanations for the current differences between sites could include the way habitat complexity is distributed over the studied altitudinal range and the nature of annual climatic differences, are probably the keys to this apparent lack of phenomological homogeneity (see Happold and Happold, 1992; Patterson et al., 1998). Historical explanations could include the altitude, glacial history, and past inter-connections with other areas (Vuilleumier and Simberloff, 1980; Patterson et al., 1998; J. Patton, pers. comm.).

Tropical ecosystems are generally characterized by high species diversity, high equitability, low numbers of individuals, temperate ones by with lower species diversity, skewed equitability, and higher numbers of individuals (Glanz, 1982; O'Connell, 1982; Claridge et al., 1997). The relatively low mean trap success (9.76%), higher equitability (the numerically dominant species, *A. mollis*, comprising 29.8% of specimens), and higher species diversity of the montane forest small mammal fauna contrast with that of the páramo (mean trap success 23.3%; 75.5% *A. mollis*). These indicators show that, while the montane small mammal communities may be structured like tropical systems, that of the páramo more closely resembles a temperate situation (see O'Connell, 1982). This has also been observed for certain groups of Andean plants (Simpson, 1974), reptiles and amphibians (Duellman, 1979), and birds (Vuilleumier, 1986).

Reig (1986) compiled a list of rodents living in one or more of the 23 páramo areas of the northern Andes recognized by Vuilleumier and Simberloff (1980). He did not make comparisons between the localities nor provide separate lists for various sites, but listed 27 species overall. With nine páramo species, Cajas would appear to have a good representation of northern Andean high-altitude rodents. The taxonomic spread of Cajas's páramo rodents (1 oryzomyine, 3 thomatomyine, 1 ichthyomyine, 2 akodontine, 1 phyllotine, and 1 sigmodontine), when compared to rodent communities in Peru (e.g., Pearson and Ralph, 1978; Patton, 1986), does not support Reig's (1986) contention that, while akodontines and phyllotines are the most speciose myomorph rodents in puna habitats, the Oryzomyini are the most speciose in páramo.

## SPECIES ECOLOGY

### Marsupials

*Caenolestes caniventer* Anthony, 1921 and *C. tatei* Anthony, 1923.—On 9 September 1983, a pregnant female (1+1)<sup>14</sup> of *Caenolestes caniventer* (see Fig. 5) was caught in one of 20 snap traps placed in shrubby secondary forest in the Rio Mazán valley. Three days later, a specimen of *C. tatei* was taken in the same

<sup>14</sup> i.e., one embryo in each uterine horn.

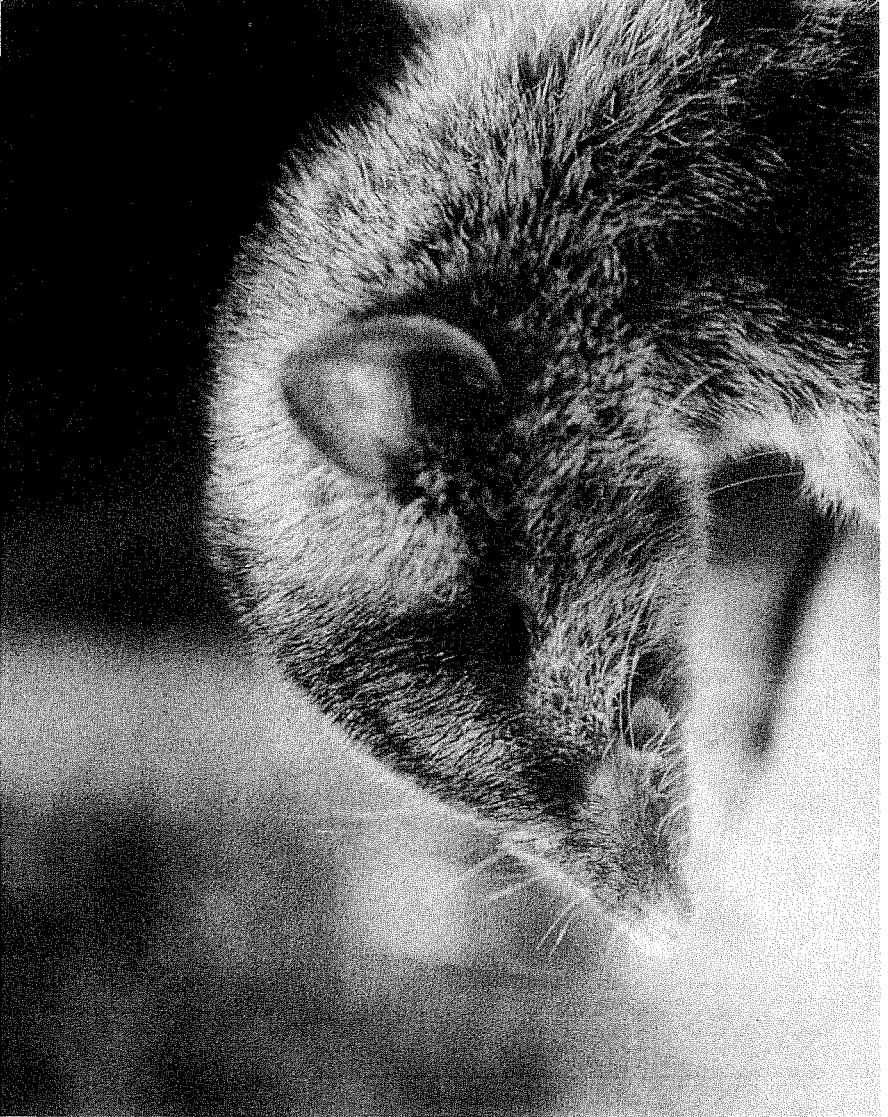


Figure 5. *Caenolestes caniventer*. Photograph, Adrian Barnett.



habitat type on a moss-covered branch some 2 m from the ground. Both species are comparatively little-known. Such habitats are known to be favored by caenolestids (see references in Barnett, 1991). Caenolestids can be locally common (Kirsch and Waller, 1979). However, trapping in subsequent years on the Cajas Plateau found no more specimens, in neither the primary nor secondary forest of Mazán, nor the other montane forest site at in the Zorracucho Valley. Nor were they caught on the páramo, supporting the contention of Hunsaker (1972) that both these marsupial species are exclusively montane forest species.

*C. caniventer* is widely distributed, extending from central Andean Ecuador (Eisenberg and Redford, 1999) to northern Peru (Pacheco et al., 1995). *C. tatei* has a much more localized distribution. Barnett (1991) has pointed out that the Rio Mazán valley is very close to G.H.H. Tate's original collection site for *C. tatei*, Molleturo, Azuay Province (see Anthony, 1921), and suggested that *C. tatei* may be endemic to this massif. The recently described *Caenolestes condorensis* (Albuja and Patterson, 1996) also shows this pattern of restricted distribution on a single massif, being confined to the Cordillera del Cóndor, southeastern Ecuador.

### Insectivores

*Cryptotis montivaga* Anthony, 1921.—Twelve specimens of *C. montivaga* were trapped. One was taken in montane forest, five in quenoa forest, and six in streamside scrub (including one in the páramo/forest ecotone at Chirimanchi). None was taken in open grassland habitats (see Barnett, 1992). These preferences are similar to those recorded for *C. thomasi* (Durant and Péfaur, 1984; Lopez-Arevalo et al., 1993) and *C. meridensis* (Durant and Díaz, 1995). Head and body length of trapped specimens of *C. montivaga* varied between 65 mm and 86 mm. Weights varied between 9 g and 16 g, making *C. montivaga* one of the largest members of the genus. This may be associated with the altitude at which it lives, for it is the highest-living member of the genus, and metabolic constraints on small-bodied insectivores are severe under the climatic conditions prevailing at high altitudes (see Choate, 1970; Doucet and Bider, 1974; Pankakowski, 1979; Churchfield, 1990; Barnett, 1992).

It is common for shrews to die of fright in live traps (Orr, 1949; Churchfield, 1990; Lopez-Arevalo et al., 1993). However, the montane forest specimen (weighing 10 g when captured) was captured alive in a streamside live-trap set for *Chibchanomys*. It was maintained in captivity for several days, allowing a unique opportunity for observation (there being no other data on the behavior of this species). It ate grasshoppers, crickets, staphylinid, chrysomelid and ruteline beetles, muscid dipterans, hemipterans, hairless caterpillars, small moths (including Pterophoridae, Pyralidae and Tortricidae), phasmids, and earthworms. All were killed by a bite to the 'neck.' After initial investigations, it avoided harvestmen (Phalangida), ants, and hairy caterpillars. It was unable to deal with the heavy armour of scarabaenid beetles or larger members of the Rutelinae, and

became mired in the wing-scales of large moths. It ate up to 2 g of food in a two hour period. As noted by Churchfield (1990), food-finding in many Soricidae appears to be largely a matter of chance. These observations compliment the preliminary data on the diet of *C. montivaga* presented by Barnett (1992), who noted that the contents of five stomachs included beetle elytra, spider legs, and caterpillars.

Of the five females caught, two were lactating (NHM 84.338, 87.919: caught on 29 August 1983 and 28 July 1984, respectively) and one (now in the collection of the Esuela Polytechnica Nacional, Quito, trapped 20 August 1981; head and body 82 mm, weight 16 g) was pregnant with 2 embryos (1+1). Lopez-Arevalo et al. (1993) reported *C. thomasi* in Colombia breeds in these months. However, this period represented the rainiest time at their eastern Cordillera study site, unlike Cajas, where these are the driest months.

A preliminary report in Barnett (1992) on the litter size of *C. montivaga* has now been supported by three additional observations. In each case the females had two embryos. In Barnett (1992) I pointed out that *C. montivaga*'s observed litter size was low compared to the rest of the genus *Cryptotis* (see Choate, 1970; Mock and Conway, 1975). Relating it to the rigours of insectivorous life at high altitude, I ascribed the small litter-size to K-selection. I now believe this is more likely to be due to adversity-selection, the form of investment-mediation in offspring that operates in predictably severe environments (see Southwood, 1977), being (in the case of *C. montivaga*) a consequence of lactational stress (see Sikes, 1995; Rogowitz, 1996)<sup>15</sup>. This result and rationale runs counter to early studies (e.g., Dunmire, 1960) that suggested that litter size might increase with increasing altitude as a compensation for a shorter period of reproductive activity.

Marshall (1980), pointing out that the extinction of the most specialized caenolestids (of the sub-family Adberitinae) was contemporaneous with the invasion of the Neotropics by placental insectivores, believes that ecological similarity and competition was the cause of their demise. Extending this notion, Barnett (1992) posited that the low numbers of *C. montivaga* trapped in montane forests at the Rio Mazán were due to scramble competition for insects with the area's caenolestid marsupials (sub-family Caenolestinae). This is supported by reports from wildlife filmmakers Jim and Teresa Clare (pers. comm.) that *Cryptotis* is common in dense secondary forest around Hacienda Majan, near Molleturo (2318 m). They reported that caenolestids are rare or absent from this property. A similar habitat separation was recorded by Lopez-Arevalo et al. (1993) for *Cryptotis thomasi* and *Caenolestes obscurus*.

*C. montivaga* was originally described by Anthony (1921) from specimens collected at 3050 m near Bestión, Azuay Province, Ecuador. When collected the specimens from Cajas were the second known series. Skulls in owl pellets from Podocarpus National Park, Loja (A. Barnett pers. obs.), indicate that the species ranges farther south than both these sites. *C. montivaga* was formerly considered

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<sup>15</sup> this is consistent with the recent report by Woodman and Timm (1999) of 4 embryos in *Cryptotis goodwini magnimana*, an animal known from forests at 1730 m.

the most southerly known Neotropical insectivore (see Barnett, 1992). However, this mantle now rests with *Cryptotis peruviansis*, recently described by Vivar et al. (1997) from northern Andean Peru.

### Rodents

*Akodon mollis* Thomas, 1894 and *Akodon orophilus* Osgood, 1913 -- Together these two species comprised 70.8% of all identified animals (342 specimens; 117 in montane forest, 225 in páramo) and were numerically dominant in all habitats types, except streams and quaking bogs. Robert Voss (1983, 1988, pers. comm.) obtained similar results in northern Ecuador. Luis Albuja found *Akodon aerosus* to be the most abundant small mammal of the Cordillera del Cóndor (see Schulenberg and Awbrey, 1997: 73) and James Patton (pers. comm., 1998) reports trapping 150 individuals with 35 museum special snap traps in one 36 hour period in less than one hectare of high-altitude bunch grass. In Cajas, most páramo specimens (208, 92.4%) were taken in cover (quebradas, streamsides, and quenoa), and only 17 (7.6%) were taken out in the grasslands of the páramo. Dorst (1958) found that both *Akodon* (now *Chroecomys*) *jelskii* and *A. boliviensis* also preferred sheltered habitats.

All specimens from Cajas were originally assigned to a single species, *A. mollis*. However, following comments from James Patton (pers. comm.), specimens were re-examined, revealing the presence of several specimens of *A. orophilus* in the collection. Formerly considered a subspecies of *A. mollis*, this taxon is now considered a full species (Myers et al., 1990; Patton and Smith, 1992). The presence of *A. orophilus* in Cajas is a new species record for Ecuador and constitutes a range extension of some 250 km from the species' previously known northerly limit in northern Peru (see Cabrera, 1961; Myers et al., 1990; Patton and Smith, 1992; Wilson and Reeder, 1993).

The ecology of the genus *Akodon* appears to closely resemble that of the temperate genus *Microtus*, to which, superficially, *Akodon* bears a strong external resemblance (see Fig. 6). Several members of the genus have been well studied (see references below), but both *A. mollis* and *A. orophilus* appear to be little known. From data in Cabrera (1961), Nowak (1999), Eisenberg and Redford (1999), and examination of the NHM collection, *A. mollis* would appear to be one of the highest-living members of the genus. Specimens varied from 75 mm-118 mm in head and body length. The tail is always shorter than the head and body (63 mm-88 mm). Weight varied from 15.5 g for sub-adult males to 43 g for a pregnant female.

An analysis of fecal pellets from 17 *A. mollis* and 6 *A. orophilus* from Cajas across a range of head and body lengths found both plant and insect remains in the diet. Insect remains varied from 10% to 70% by volume per individual. These figures closely resemble those obtained by Barlow (1969) for *A. azerae*, where an



Figure 6. *Akodon mollis*. Photograph, Adrian Barnett.

analysis of 11 stomachs found 70% invertebrates and 20% plant material (see also Eisenberg and Redford, 1999).

This dietary data, combined with ubiquity and high numbers in all habitats (see Table 3) indicate that, in Cajas, *A. mollis* is a widespread and abundant generalist. Such an ecology resembles that of other akodontines (*Chroeomys andinus* in Peru, Pearson and Ralph, 1978; *A. azarae* in Argentina, Dalby, 1975; Apfelbaum and Blanco, 1985a; Ellis et al., 1997; *A. boliviensis* in Peru, Dorst, 1958; *A. delores* in Argentina, Apfelbaum and Blanco, 1985b; Piantanida, 1987; *Abrothrix olivaceous* in Chile, Fulk, 1975; Murúa and González, 1985; Simonetti et al., 1985; Meserve and Le Boulenge, 1987; Murúa et al., 1987; *Abrothrix longipilis* in northern Chile; Glanz, 1984).<sup>16</sup> *A. orophilus*, by contrast, appears to occur at comparatively low densities in closed cloud forest habitats.

The two species appear to show ecological separation. All specimens taken in the Podocarpus forests at Mazán were *A. orophilus*, while those in the adjacent grazed grassland were *A. mollis*. In the Zorracucho Valley, *A. orophilus* was taken in the secondary forest on the sides of the valley while *A. mollis* occupied the grazed grasslands of the valley floor. However, *A. orophilus* was not caught in páramo, and there all the akodons caught in quenoa forest were *A. mollis*, indicating it is another factor (possibly temperature) rather than cover that limits the upper altitudinal range of *A. orophilus*.<sup>17</sup>

Species of *Akodon* have been variously reported as diurnal, nocturnal, crepuscular or active at any time of day (Eisenberg, 1989; Emmons, 1997; Nowak, 1999; Eisenberg and Redford, 1999). *A. mollis* appears to be predominantly nocturnal. Of 225 individual *A. mollis* trapped on the páramo, only nine (4.0%) were found during mid-day trap checks.

Reproductive data does not appear to have been recorded before for *A. mollis* nor for *A. orophilus*. No pregnant *A. orophilus* were captured, but three *A. mollis* females were pregnant when trapped. Each carried two embryos (1+1). Other members of the genus usually have three to four young (Nowak, 1999; Eisenberg and Redford, 1999). As with *Cryptotis*, this difference may be attributable to adversity selection (Southwood, 1977), a consequence of life at high altitudes (see also Badyaev, 1997). A specimen of *A. mollis* collected in Loja (3 June 1899, unaccessioned NMH specimen), was recorded by its collector, P. O. Simons, as having four embryos. Significantly, the collection altitude (2100 m) is much lower than for any of the pregnant Cajas specimens, supporting the adversity selection position. A study by Krohne (1980) on *Microtus californicus* populations under conditions of distinctly different adversity (perennial native grasslands and introduced annual grasslands), provides a supportive parallel to the *Akodon* results. From Southwood's (1977) model one would predict that *A. orophilus* would have

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<sup>16</sup> several of these were considered to belong to the genus *Akodon* when the papers in question were written (e.g., *Ab. olivaceous* and *Ab. longipilis*, see Spotorno et al., 1990; *Chroeomys andinus*, see Patton and Smith, 1992).

<sup>17</sup> a species whose fur is both shorter and less dense than that of *A. mollis*.

larger litters than *A. mollis*. It is to be lamented, therefore, that no reproductive data is available from *A. orophilus* in Cajas to test this assertion at a local level.

Overall, 80% of *Akodon* captured in Cajas were juveniles (76.7% for *A. mollis* and 83.3% for *A. orophilus*). Most (70%) of the adults collected were caught in the last third of the fieldwork season. This suggests that *A. mollis* may have two litters a year and a bimodal breeding season. This reproductive pattern has also been reported for a number of other members of the genus (Nowak, 1999). It is possible there is little temporal overlap between reproductive generations of *A. mollis* (as also reported for *Akodon* spp. by Meserve et al., 1990) so that, during August-September, the Cajas population is entering a second reproductive period, with juveniles being a result of a preceding reproductive peak (see also Zuleta and Bilenca, 1992). Dalby (1975) reported the average gestation time of *A. azarae* to be 22.7 days and the time to first breeding to be 2 months. If the time-scales of *A. mollis* are similar, this would place the other reproductive peak around May-June, the time of highest rainfall on the Plateau (see Meteorological Office, 1977; Ramsay, 1992). On a number of other Andean páramos this has been shown to be the period of greatest bio-productivity (Ramsay, in press, Ramsay and Oxley, in press), reflecting peaks in both fresh plant growth (Sturm and Rangel, 1985; Ramsay and Oxley, 1996), and insect abundance (Sturm, 1979; P. Ramsay pers. comm., 1998).

Osgood (1914: 164) noted that grassland populations of *A. m. orophilus*<sup>18</sup> resembled *Microtus* with "labyrinthine runways, open burrows, and fresh grass cuttings," while "in heavy woods or rocky stream beds the[y] lead wandering lives, and have as retreats only natural openings." Data from the current study supports this observation. No akodonts were trapped from burrows in montane forest or in quenoa forest. However, on the páramo, they were trapped on several occasions emerging from holes. These frequently had small mounds of fresh vegetation and grass seed heads piled next to them. The burrow entrances often occurred in aggregated groups of a dozen or so. During the day most would be sealed with a cap of earth. Dorst (1958) observed cut vegetation by and within the burrows of *A. boliviensis*.

The importance of melanic variation in pelage coloration in *A. mollis* has been difficult to determine. Writing of color variation in *A. mollis*, Hershkovitz (1940a: 1) noted that "despite the diversity of their habitats, populations of this mouse exist practically undifferentiated [from] the inter-Andean Plateau ... nearly [to] the snow line." There was concordingly little variation in specimens from Cajas, variation being limited to some animals with a wide, ill-defined dorsal stripe. However, four very dark specimens were taken at Yakatuviana (NHM 82.808, 82.809, 84.292, 84.293). Partial melanism is often associated with mammal populations living in moister warmer environments such as occur at Yakatuviana. Osgood (1914), for example, named *A. mollis orientalis*<sup>19</sup> from dark-

<sup>18</sup> now considered a sub-species of *Akodon orophilus* (see Patton and Smith, 1992 page 91).

<sup>19</sup> now considered a sub-species of *Akodon orophilus* (see Patton and Smith, 1992 page 91).

furred specimens from the humid montane forests of north-eastern Peru, and Sanborn (1947) noted that *inambarii*, a dark subspecies of Peruvian and Bolivian *Chroeomys jelskii* (formerly *Akodon jelskii*), came from an area that is notably wet and cloudy.<sup>20</sup> However, examination of 244 Ecuadorian *A. mollis* skins in the NHM collection revealed very few other melanics or partial melanics. Examination of another 261 specimens from 14 other *Akodon* species revealed no within-species pattern of pelage color variation that could be associated with habitat.<sup>21</sup> Like the NHM's leucystic specimen of *A. olivaceus* in the same collection (NHM 7.2.12.1), the specimens from Yakatuviana should perhaps be best considered sports and undeserving of subspecific status (see Owen and Shackelford, 1942; Mustrangi, 1994; Literák and Zejda, 1995 for similar examples with other species). The trapping of several similarly colored animals in the same locality may simply indicate genetic relatedness and a sharing of the same colour-coding allele (see Benton, 1953; Fedyk and Borowski, 1980 for parallel mammalian examples).

Of the 168 *A. mollis* skins presented to the NHM, 19 had white patches of fur about the head and neck (1.2%). The cause(s) of the white fur patches are unknown. They were constant in neither size, shape, nor position. Field dissections revealed neither subcutaneous parasites at these locations, nor any scars or lesions. However, white spotting is frequent in European shrews (*Sorex*) (see Puček, 1964), where it is frequently a result of intra-specific aggression, usually between males (Churchfield, 1990). Fifteen of the *A. mollis* with white spots were adult (78.9%, 6 males, 9 females), indicating that a similar explanation, combined with aggression during mating, may apply here.

***Chibchanomys orcesi* Jenkins and Barnett, 1997.**—Five specimens of this new species were captured (see Fig. 7). Two were taken on a small bush-covered island in the middle of a small, cold, clear, fast-flowing stream at 3700 m. Flowing between large boulders, the stream had a bottom of course of gravel and stones. It was no more than 40 cm deep and lacked aquatic macrophytes (see Fig. 8). Two more were caught in similar habitat at Lake Torreadora, 4000 m. A fifth specimen was caught in the Zorracucho Valley, in a broad, deep muddy stream feeding in to Lake Llaviuco. Heavy rain may have washed the animal in from higher páramo streams. Further details on habitat are given by Barnett (1997a).

No ichthyomyines are specialized for lentic waters, though Ludovic Söderstrom caught *Ichthyomys* in marshy fields (Tate, 1931), and local informants told Andrea Pogson (pers. comm.) that they had occasionally seen fishing mice (presumably *C. orcesi*) in lakes on the Cajas Plateau. The use of mid-stream islands seems a common feature of aquatic mice. Described as successful trapping sites for many ichthyomyines (see Voss, 1988; Barnett, 1997a), they have also been

<sup>20</sup> for other examples see Nowak, 1991: 658-659 on the Himalayan vole *Hyperacrius*; Rosevear, 1969, 1974; Barnett and Prangle, 1997 for examples with African mammals.

<sup>21</sup> though, as J. Patton (pers. comm.) has pointed out, all of the Andean wet forest *Akodon* (*aerosus*, *fumeus*, *kofordi*, *mimus*, *orophilus*, *siberiae*, *surdus*, *torques*) are dark in comparison to open grassland species (*boliviensis*, *juainensis*, *lutescens*, *mollis*, *subfuscus*).



Figure 7. *Chibchanomys orcesi*. Photograph, Jim Clare.





Figure 8. Habitat shot for *C. orcesi*. Near Lake Torreadora (4000 m). Photograph, Adrian Barnett.

found to be so for their ecological equivalents in the Paleotropics (e.g., see Osgood, 1928).

This new species (Jenkins and Barnett, 1997) was named in honor of Gustavo Orcés, a pioneer of Ecuadorian vertebrate biology.<sup>22</sup> Its ecology, natural history, and biogeography were discussed by Barnett (1997a). Like *Caenolestes tatei*, it is believed to be endemic to the Cajas Plateau (Barnett, 1997a). It is the sixteenth known ichthyomyine (see Voss, 1988; plus Ochoa and Soriano, 1991) and the sixth member of its tribe known from Ecuador, making that country the most speciose for this tribe.

In his review of the Ichthyomyini, Voss (1988) gives the distribution of the other member of the genus, *C. trichotis*, as the highlands of the Tachira Andes, Venezuela, the Colombian Cordillera Oriental, and the Cordillera Carpish in Peru. *C. orcesi* appears to occur at just one locality within the range of these widely separated populations. Barnett (1997a) provided an analysis with examples of parallel biogeographical patterns in other taxa, including birds, small mammals, and bromeliads. However, Paulina Jenkins used the PAUP program (Swofford, 1990) to compare the features shared by *C. orcesi*, the Peruvian "*C. trichotis*," and Colombian-Venezuelan populations of *C. trichotis*. Her data reveal that the Peruvian population may, in fact, be more closely related to *C. orcesi* (see Jenkins and Barnett, 1997). Though this pattern does not occur in all taxa (see Pearson, 1982; Reig, 1986; Albuja and Patterson, 1996; Vivar et al., 1997), this Peruvian-Ecuadorian/Colombian-Venezuelan distribution pattern is also far from unusual in high altitude vertebrates, with the Huancabamba Depression acting as a distributional barrier (see Duellman, 1979; Fjeldså and Krabbe, 1990 for parallel herpetological and avian examples, respectively)<sup>23</sup>.

Stomach contents of three specimens showed fish and larvae of aquatic insects. Observations of a captive specimen by J. and T. Clare revealed the animal could actively hunt for fish underwater. The small eyes and enlarged vibrissae make tactile location the most feasible form of hunting. The ecology of this species, like most of the tribe, closely resembles that of the Old World otter shrews (*Micropotomogale lamottei*, *M. ruwenzorii*, and *Potomogale velox*; see Kingdon, 1997, for an account). The African lowland murine *Colomys goslingi* also shows similarities in feeding ecology (Dieterlen and Statzner, 1981), though it is less morphologically specialized (Kingdon, 1997).

*C. orcesi* appears to be quite rare. Persistent trapping in appropriate localities over several years by two separate study groups yielded very few specimens (see Barnett, 1997a). In each case animals were trapped from the same localities, and not from other, apparently suitable ones. The species therefore appears to have both low population density and restricted habitat preferences. Also, it is only known from the Cajas Plateau (Barnett, 1997a; Jenkins and Barnett, 1997). Together these factors provide cause for conservation concern. Small riparian mammals are

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<sup>22</sup> it is the second higher vertebrate named in his honor, see Ridgely and Robbins (1988).

<sup>23</sup> Vivar et al. (1997) believe that this 'pattern' may be (partly) explained by sampling bias, reflecting the paucity of work in this border region.

frequently at risk from anthropogenic habitat changes (R.G. Anthony et al., 1987; Galindo-Leal, 1997). Barnett (1997a) has cited reasons why *C. orcesi* populations in Cajas may be threatened. These include burning, grazing and increased tourist pressure. However, such concerns should not be given uncritically. Louise Emmons (pers. comm., 1997) has received reports of the Central American ichthyomyine *Rheomys* being observed in quite polluted water, and Tate (1931) reported *Neusticomys* from irrigation ditches.

***Microryzomys altissimus* (Osgood, 1933) and *M. minutus* Tomes, 1860.**—Thirty *M. altissimus* and two *M. minutus* were trapped. The relative numbers may have little overall significance, for Durant and Díaz (1995) have reported that *M. minutus* numbers show great seasonal variation. Along with *Thomasomys gracilis* (see below), *M. minutus* is the smallest rodent on the Plateau, with individuals being recorded from 9.5 g. *M. minutus* was taken in secondary forests around Lake Llaviuco in the Zorracucho valley (3100 m). *M. altissimus* was also found below the tree-line (two records from Zorracucho) and in the shrubby forest/páramo ecotone trapped at Chirimanchi, but was most common in the páramo. On the páramo most records come from sheltered habitats (rocky outcrops, 9; *Polylepis* forests, 7; streamside scrub, 6; quebradas, 3). The animal was infrequent on the exposed páramo grasslands (3 of 28 records). This preference for sheltered habitats is shared by the shrew *Cryptotis montivaga* (see above) and páramo-living species of *Caenolestes* (see Gregory, 1922; Tate, 1932a).

Based on museum specimens, Carleton and Musser (1989) have noted that the range of *M. altissimus* extends to higher altitudes (to 4500 m), and *M. minutus* favors altitudes between 2000 and 3500 m. Handley (1976) and Osgood (1933) both record *M. minutus* almost exclusively from montane and cloud forests (the latter as *aurillus*). Where *M. minutus* does enter the páramo zone, it is restricted to heavy cover such as is offered by *Polylepis* and *Espeletia* thickets (the field notes of R. Voss, quoted by Carleton and Musser, 1989: 56-57). Based on analysis of over 900 museum specimens from 200 collecting localities, they report that 75% of the records for *minutus* are concentrated between 2000 and 3500 m, while 80% of the records of *altissimus* occur between 2500 and 4000 m. They record that a zone of sympatry exists between the two species near the tree-line. At 3100 m, the records from Zorracucho are in agreement with this synopsis.

The two species are difficult to separate, both in the field and in the museum. However, field experience has shown that, while *minutus* generally has a monocoloured tail, *altissimus* has one which is bicoloured, dark above (see Barnett and Moleon, 1999). This has also been observed in museum material by Carleton and Musser (1989), who have also made helpful observations on the differences in shape and arrangement of the planar pads and in the shape of the hind foot, characters that may also be used to distinguish these two species in the hand. Carleton and Musser (1989) also report the tail to be proportionately longer (145% vs. 137% of hb) in *M. minutus* than in *M. altissimus*. Eisenberg and Redford (1999) provide characters of the palate for distinguishing skulls of the two species.

Fifteen of the *M. altissimus* specimens were immature. One male (NHM 82.732, caught 7 August 1983) had scrotal testes, one female had a perforate

hymen (caught 16 July 1983). Neither of the *M. minutus* were in breeding condition.

*Oligoryzomys destructor* (Tschudi, 1844).—Five specimens (3 males, 2 females) were trapped. All specimens came from the Zorracucho Valley (3100 m). Other than an avoidance of grasslands trapping data gives little indication of habitat preference by this species. One individual (NHM 84.300) was caught on the mixed mud and gravel banks of the same unnamed stream that yielded *Chibchanomys orcesi* (see Barnett, 1997a). An adult female (NHM 84.303) was living in human habitation. One juvenile male (NHM 84.299) was taken on an open disturbed wooded slope with sparse ground cover, no streams and dry exposed soil, while another (NHM 84.302) was taken on a stream-rich slope with thick vegetation and mossy groundcover beneath scattered *Eucalyptus globulus*. Examination of labels of specimens in the NHM collection shows a similar variability in recorded habitat preferences throughout the collection, with references to forest (NHM 15.7.12.21), a hedge (NHM 15.7.12.20), a house (NHM 14.4.25.25), streamside (NHM 27.11.1.110), and swampy grassland (NHM 14.4.25.65). Most Ecuadorian *O. destructor* specimens in the museum collection do not come from altitudes as high as those at Zorracucho, being more commonly taken around 2900 ft ( $\approx$  1000 m). Hershkovitz (1940b) recorded this species (as *O. spodiurus*) from 1500 m in the sub-tropical forests of Ecuador's western Cordillera. Osgood (1914) reported it (as *O. stolzmanni maranonicus*) from dense humid forests and town gardens in north-eastern Peru.

*Oryzomys albigularis* Tomes, 1860.—Sixteen *O. albigularis* were obtained. This beautiful rodent is one of the largest on the plateau, weighing up to 79 g with a head and body length of up to 162 mm and a tail length of 170 mm. All belong to the subspecies *albigularis*. Members of this subspecies are distinguished from *O. a. moerax* by their belly colour (paler in *albigularis*) and the presence of a throat patch where the hairs are pure white to the base (a feature absent in *O. a. moerax*)<sup>24</sup> (see Gyldenstolpe, 1932: 14). On Cajas specimens of *O. albigularis* were trapped only in cloud forest, a habitat preference also reported by Osgood (1914), Handley (1976), Ashe and Timm (1987), and Eisenberg and Redford (1999). It appears to prefer dense cover (Osgood, 1914). Durant and Díaz (1995) reported that this species was at its lowest density in the wet season. Such seasonal fluctuations may explain why, while Péfaur and Díaz-de-Páscual (1985) reported *O. albigularis* as the numerically dominant species at northwest facing montane forest sites between 1000 and 2500 m, it was the rarest species in Zuñiga et al. 's (1983) study.

Six of ten males were of adult size, four were in breeding condition (NHM 82.725, 82.276, 84.306, 84.308). A female (NHM 84.305), taken on 3 September 1983 was lactating. Two of the specimens were retrieved from a number of *O. albigularis* found dead on a path at Yakatuviana. Though suffering some insect damage, all were otherwise unmarked. No reason could be found for this phenomenon. Interestingly enough, in the original description of the species Tomes

<sup>24</sup> NHM specimens examined: 54. 413 to 417, 54.419, 13.10.2.88.

(1860: 265) noted that the holotype and topotype were both found under similar circumstances, lying dead on a [forest] path among a number of other of dead conspecifics. Examination of these specimens (inc. NHM 7.1.1.1.106) shows they also lack obvious external damage. None of the females trapped in Cajas were pregnant. Timm et al. (1992) have recorded litter size in this species as three.

It has long been known that this species had a species of staphylinid beetle *Amblyopinus* in its fur (e.g., Seevers, 1950). This association has been shown (Ashe and Timm, 1987; Timm and Ashe, 1987) to be commensal rather than parasitic, with the beetle feeding on such ectoparasites as mites and fleas in the rodents fur. The number of beetles has recently been shown to vary between sexes and ages of these rodents (Barnett, 1997b; Barnett and Shapley, in prep. b)<sup>25</sup> in accordance with predictions of theories of androgen-mediated immuno-suppression and sex-bias in mammalian ectoparasite loads (Schalk and Forbes, 1997). As far as we know, this is the first time such an indirect effect has been shown.

*Phyllotis andium* Thomas, 1912 and *Phyllotis haggardi* Thomas, 1908.— These are the most northerly of the 11 species in the genus *Phyllotis* (Pearson, 1958, 1982; Braun, 1993; Nowak, 1999). One *P. andium* and six specimens of *P. haggardi* were taken. The two species are easily separated in the hand (Barnett and Moleon, 1999). *P. haggardi* has a bicoloured tail that is usually greater than 95 mm in adults, whereas *P. andium* has a unicoloured tail that is usually less than 85 mm. Only one female *P. haggardi*, an immature, was trapped (NHM 82.811). Three of the five males captured were mature and in breeding condition (NHM 82.812, 84.344, 84.345).

One *P. haggardi*, a young male, was found living commensally in the warden's hut at Lake Torreadora. All other specimens were taken in or around rocky outcrops or stony ridges in otherwise open páramo where the shrub cover was limited. All captures were made at night. Though taken at the same altitude, the two species were not sympatric. There were substantial habitat differences, with the single *P. andium* taken from amongst *Hieracium* and *Baccharis* bushes in a shallow shrub-rich valley, while *P. haggardi* occurred in rockier more exposed habitats. In Peru, Dorst (1958) found similar habitat separation occurring between (respectively) *Phyllotis pictus* and *P. darwini*. According to Pearson (1958, 1972), *P. andium* inhabits brushy habitats, but neither he, Anthony (1924a), Braun (1993), nor Eisenberg and Redford (1999) give any indication of habitat preferences for *P. haggardi*.

*P. haggardi* was previously known only from north-central Ecuador (Wilson and Reeder, 1993; Eisenberg and Redford, 1999),<sup>26</sup> making the records from Cajas range extension for the species of several hundred kilometers.

Cajas is unusual in the phyllotine component of its small mammal community. *P. haggardi* is endemic to Ecuador and is at its southern limit in Cajas, while *P. andium* is close to its northern limit there (see Pearson, 1972;

<sup>25</sup> manuscript available from author on request.

<sup>26</sup> contra Pearson (1972) and Braun (1993) who believed it to occur in southern Ecuador also.

Braun, 1993). The zone of overlap between the two species is only some 110-160 km long and is further restricted by altitude; while *P. andium* ranges widely from 200 to 4800 m, *P. haggardi* occurs only between 2000 to 4500 m (see Pearson, 1958, 1972; Braun, 1993: table 1). This may account for Pearson's (1982: 273) opinion, now obviously erroneous, that the two species do not occur in the same geographical location. According to Pearson (1958: 441), in *P. haggardi* there is a trend of "increasing duskiness to the south, together with an increased length of the skull and lengthening of the nasals" (see also Anthony, 1924a). He uses the appellation *P. h. fuscus* for southern populations, including those in the Cajas region.

***Sigmodon inopinatus* Anthony, 1924.**—Five specimens of *S. inopinatus* were trapped. All were taken near water; one in a hole in a riverbank quebrada at Chaupiurcu (3750 m), another in a marshy area at Lake Torreadora (4000 m), and three others on a dense reed mat forming a quaking bog in the middle of a shallow unnamed lake near Lake Torreadora. Surface runs were wide and obvious at the reed mat trap site. Similar habitat preferences and run-making behaviour have been reported for *S. hispidus* (e.g., Mazzotti et al., 1981; Fitzgerald, 1983) and *S. alstoni* (Voss, 1992). No nests were seen.

One female specimen (now in the collection of the Escuela Polytechnica Nacional, Quito) taken on 19 July 1984 had four embryos (2+2). This is at the lowest end of litter size variation in *Sigmodon* (see Randolph et al., 1977; Mattingly and McClure, 1982) and, since *S. inopinatus* is the highest-living member of the genus (see Voss, 1992), may be attributable to the same adversity-selected suite of traits also believed to be governing small litter size in *Cryptotis* and *Akodon* in Cajas (see Southwood, 1977). In the only other datum point for this species, a litter of four is also reported by Anthony (1924b) from the type specimen of the species, the largest individual in a series of 11 specimens. Nipple number is lower in *S. inopinatus* than in other members of the genus (Voss, 1992).

*S. inopinatus* shares many aspects of the ecology of its close relative *S. hispidus* (see Voss, 1992). However, while *S. hispidus* is the most abundant member of the small mammal community in many parts of its wide range (Sietman et al., 1994; Doonan and Slade, 1995; Stokes, 1995), relatively low numbers of *S. inopinatus* were found at Cajas. This may be due to competition with the numerically dominant *Akodon mollis*. Though smaller, *A. mollis* appear to share a similar ecology to *S. inopinatus* and may have excluded it from some habitats. Such interactions have been recorded at various locations in the extensive range of the genus *Sigmodon* (Glass and Slade, 1980; Putera and Grant, 1985; Davis and Ward, 1988; Voss, 1992). Such interactions may be especially important in Cajas where populations of *S. inopinatus* would appear to be at the southern limits of both the species' and genus' range (see Voss, 1992)<sup>27</sup> and hence possibly a less effective competitor (see Grant, 1972, who includes a discussion of competitive exclusion effects at range limits in rodents).

<sup>27</sup> Only *S. peruanus*, which extends into northern Peru, occurs further south (Pacheco et al., 1995; V. Pacheco pers. comm., 1999).

The records of *S. inopinatus* at Cajas challenge an evolutionary scenario for the species proposed by Reig (1986). The type series of *S. inopinatus* was taken by G.H.H. Tate in October 1923 at Urbina at 11,400 ft (3508 m) on the slopes of Mt. Chimborazo (Anthony, 1924b). The Cajas specimen series is the second ever for this species (Voss, 1992) and represent a southerly range extension of around 200 km. According to Reig (1986), the genus arose in north-central Peru from a *Neotomys*-like ancestor and moved northwards to its current distribution, via Andean valleys. Reig (1986: 430) proposes that *S. inopinatus* is a relictual and historically isolated species that "is likely to have arrived [on the páramos of Chimborazo] by the uplifting of the páramos during Plio-Pleistocene times," presumably while this northward migration of the genus was in progress. With the discovery of the species at Cajas, such a site-specific explanation is clearly no longer required, especially since it is likely that further trapping will find the species at other suitable habitats between the two currently known localities.

Though named as a full species by Anthony (1924b), this taxon was (with the exception of Reig [1986] who accepted its original status), generally considered a subspecies of *Sigmodon hispidus* until Voss' revision of the genus (Voss, 1992). Noting that the long silvery rump hairs were not diagnostic as Anthony (1924b) proposed, Voss (1992) provides a series of cranial, dental, and chromosomal characteristics to support his re-elevation of this taxon to specific status (*contra* Hershkovitz, 1955; Cabrera, 1961). The parapatric *S. peruanus*, also recorded from Azuay Province, is found only in lower altitudes and more xeric habitats (see Voss, 1992).

***Thomasomys* spp.**—Six species of *Thomasomys* were taken: *T. aureus* (Tomes, 1860), *T. baeops* (Thomas, 1899), *T. cinnameus* Anthony, 1924, *T. gracilis* (Thomas, 1917), *T. paramorum* Thomas, 1898, and *T. pyrrhonotus* Thomas, 1886. Only *T. cinnameus* occurred in páramo alone. *T. pyrrhonotus* and *T. gracilis* were taken in páramo and montane forest. The other three species were taken only in montane forest.

The páramo-living species of *Thomasomys* appear to favor sheltered areas. Based on trappability, Anthony (1924b) believed *T. cinnameus* to be rather rare. Instead, results from Cajas indicate it is a quenoa forest habitat specialist. In the current study, four of the six *T. cinnameus* were caught in minimally disturbed quenoa forests, all on the ground in areas with dense canopy and little groundcover but deep moss. The two other specimens were taken in a dense isolated clump of composite bushes on an exposed slope covered with tussock grass. It was the only member of the genus to be found solely in páramo.

Three specimens of *T. pyrrhonotus* were taken in degraded quenoa forests with open canopies and heavy shrub layers. Two *T. pyrrhonotus* specimens from montane forests were also taken in degraded vegetation (one on an open wooded slope, the other among rocks in a grass-covered area logged some five years previously). Osgood (1914) also caught this species both above the timberline and in cloud forest.

Of 25 *T. gracilis* trapped, 21 (74.4%) were from habitats in the páramo. Though several *T. gracilis* were trapped in sheltered areas such as dense scrub, streamsides, quebradas, and rock jumbles in páramo grassland, as well as in quenoa forests, none was taken in open, exposed páramo grassland. Some were taken in degraded, open-canopied quenoa forest at Chaupiurcu, but only in the most sheltered parts. Both *T. pyrrhonotus* and *T. gracilis* were trapped in the lower limbs of *Polylepis* trees. Nowak (1999) indicates arboreality is common in this genus. However, otherwise terrestrial species can be attracted to baited traps set in trees (Manville et al., 1992). Such confounding effects, combined with the jumbled and topographically complex nature of this forest type (see Fig. 3), means that this may not be a true indication of regular arboreal activity for these species. Specimens of *T. gracilis* were also captured in secondary cloud forest around Lake Llaviuco in the Zorracucho Valley, where it preferred mossy-floored habitats with well-developed canopy and thick epiphyte cover.

Four *T. aureus* (see Fig. 9) were captured beneath dense shrub cover in secondary forest between 2700 m and 3100 m, another on a moss-covered log deep in primary montane forest at 2800 m, and two in very dense grass and reeds by Lake Llaviuco (3100 m). Though records from Cajas, Colombia's Reserva Biológica Carpanta (Lopez-Arevalo et al., 1993), and all specimens in the NHM are from forested areas (see also Eisenberg and Redford, 1999), Reig (1986) reported that this species may also occur in páramo. As in the current study, *T. aureus* was infrequently trapped by Lopez-Arevalo et al. (1993), where it represented less than 1% of the catch, indicating that it is either rare or difficult to trap. So little is known of the ecology of this species that I consider it worth recording that fieldnotes by Gilbert Hammond accompanying his specimens of *T. aureus* (NHM 13.10.2.28, 9.8.9.4.1, 93.10.26.1) report that the species nests in trees and feeds on fruit of the grenadilla (any of several species of shrubby montane forest *Passiflora*, Passifloraceae).

The 13 trapped *T. paramorum* came from a variety of habitats, including secondary montane forest, bamboo thickets, and scrub on recently deforested land but not (*contra* Reig, 1986) on the páramo. The common denominator for all chosen habitats seems to be moist mossy ground cover, fallen logs, and proximity to stands of *Chusquea* bamboo.

All five specimens of *T. baeops* were trapped in disturbed secondary forest sections of primary-secondary cloud forest mosaics. Preferred habitats had a dense cover of shrubs, but little arborescent canopy development. Reig (1986) listed this species solely as a páramo-dweller.

A female *T. gracilis* (NHM 82.818, head and body 103 mm, 41 g) was pregnant (1+1) when trapped on 29 July, 1981, another (NHM 84.339, head and body 86 mm, wt. 16.25 g) was lactating when caught on 21 August, 1983. Males in reproductive condition were captured between 15 and 28 August over three years. Juveniles of *T. gracilis* numbered 15 (10 f, 5 m) (based on body size, pelage





Figure 9. *Thomasomys aureus*. Photograph, Vaughan Fleming

grayness and pedal characteristics, see Barnett and da Cunha, 1998b). All juvenile *T. gracilis* were between 64 and 100 mm (mean 83.06) in head and body length (adult head and body mean = 98.0; range 86-116). Only one newly independent individual was captured (head and body 64 mm, wt 10 g). No other trapped *Thomasomys* females were pregnant. Two male *T. aureus* (NHM 84.324 and 25; head and body 170 mm and 160 mm, weights 110 g and 102 g, respectively) had scrotal testes (trapped 11 September 1983). One *T. baeops* (NHM 84.330; 104 mm, 43.5 g, trapped 4 September 1983) was lactating. One *T. cinnameus* (NHM 84.339; head and body 86 mm, w 16.25 g) was lactating when trapped on 21 August 1983, while a male (NHM 84.343; head and body 98 mm, weight 18.5 g) had scrotal testes when trapped on 28 August 1983.

Habitat distribution data indicates a size/habitat pairing occurs amongst the *Thomasomys* of Cajas. Each major habitat type (cloud forest and quenoa forest/páramo grassland) having one large and two small species: *T. aureus*, *T. baeops*, and *T. pramorum* for cloud forests, *T. cinnameus*, *T. gracilis*, and *T. pyrrhonotus* for the páramo. Head and body length has been proposed as a valid measure of ecological separation between coexisting small mammals (see Flowerdew, 1976). Size ratios for cohabiting pairs of *Thomasomys* is 1.43 for *T. baeops*/*T. pyrrhonotus* and 1.57 for *T. aureus*/*T. paramorum*.<sup>28</sup> This is close to the ratios of 1.20-1.40 first noted by Hutchinson (1959) for morphological character displacement among coexisting congeners. In each case the two smaller species are separated by habitat preference, and one large and one small species inhabit a closed-canopy arborescent habitat. Such mechanisms have been shown to structure other Neotropical small mammal communities (Fulk, 1975; Meserve et al., 1982; Vásquez, 1996) though such relationships are often complex (e.g., Meserve, 1981; Murúa and González, 1982; Ebensperger and Simonetti, 1996) and further work is required in Cajas to analyze the fine details of the interactions of the area's small mammals.

### Missing Species

Though clearly indicating a speciose locality, there are some puzzling gaps in the current list of small mammals for Cajas. These may be due to a variety of factors. As with bats (Koopman, 1978), birds (Fjeldsá and Krabbe, 1990), and amphibians and reptiles (Duellman, 1979; Lynch, 1979; Traub, 1979), the dispersal barriers of the inter-Andean basins explain the absence in Cajas of some species (e.g., *Aepomys lugens* is reported up to 3500 m, but only from the eastern Andes). The absence of others known from the western Cordillera is most likely attributable to altitude (e.g., *Ichthyomys hydrobates* to 2800 m and *Oryzomys auriventer* to 1500 m).

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<sup>28</sup> metric data available from author on request.

There are a number of species whose absence cannot be explained biogeographically, but for which possible ecological explanations exist. The semi-aquatic ichthyomyine *Anotomys leander* has been recorded from Mt. Pichincha in northern Ecuador to central Peru (Gardner, 1971). Its absence from Cajas may be due to exclusion through competition with *Chibchanomys orcesi*, which may be endemic to the Plateau (see Barnett, 1997a; Jenkins and Barnett, 1997). The altitudinal and habitat preferences of these two species overlap (see Thomas, 1906, Voss, 1988, for *A. leander*; Barnett, 1997a, Jenkins and Barnett, 1997, for *C. orcesi*). At lower altitudes, members of the tribe Ichthyomyini have been recorded in sympatry, with different species focusing on different food sources. Analysis of data in Voss (1988) shows that, in such circumstances, one species is often insectivorous, while another may have a high proportion of crab in the diet. *A. leander* and *C. orcesi* both occur at the maximum recorded altitudinal elevation for ichthyomyines (Barnett, 1997a), and at such heights freshwater crabs are lacking (see data in Barnett, 1997a). Consequently the riparian habitats of Cajas's páramo may be able to support no more than one species of this group.

On biogeographical grounds (see Gyldenstolpe, 1932; Cabrera, 1961; Eisenberg and Redford, 1999), three other species of rodent, *Rhipidomys latimanus*, *Thomasomys silvestris* and *T. cinereiventris* should occur in Cajas, but have not been found there to date. Intense efforts were made to locate *R. latimanus*, with targeted trapping in both cloud and quenoa forests for this arboreal species (see Lopez-Arevalo et al. 1993). Also, as noted previously by Barnett (1991), it is unclear why the marsupial *Caenolestes fuliginosus* was not taken in páramo traps. It is known to inhabit páramo and quenoa, and has been recorded from northern Ecuador to northwestern Peru (Tate, 1931; Albuja and Patterson, 1996), where it can be quite common.<sup>29</sup>

It should be noted that the Mountain Paca *Agouti taczanowskii* has not been recorded in Cajas, though there are records at altitudes up to 3500 m for the species to the south at Podocarpus National Park, Loja, where individuals visit human habitations (A. Barnett, M. Prangle, and B. Larssen, pers. obs.; see also Emmons, 1997) and in similar habitats in Colombia (Lopez-Arevalo et al., 1993).

### Threats to the Ecology of the Cajas Plateau:

**Alien species.**—*Mus musculus* and *Rattus rattus* were also recorded. Both were trapped in buildings, *Mus* in the warden's hut at Lake Torreadora and at an unused brewery near Lake Llaviuco and *Rattus* at the trout farm at the Llaviuco lakeside, where it was reported to be present in large numbers and feeding on stored bags of fish feed. Conversations with the area's older residents revealed that *Mus* and *Rattus* are probably recent arrivals in Cajas. Though they are currently restricted to commensal activities, there is the danger that, as has occurred

<sup>29</sup> specimens reported as *Caenolestes fuliginosus* by Barkley and Whittaker (1984) from Peru have been re-identified as *C. caniventer* (see Pacheco et al., 1995).

elsewhere (e.g., Fox and Pople, 1984; Goodyear, 1992), these alien rodents may begin to expand their range at the expense of the native species.

**Human activities.**—Unlike areas of lowland Ecuador (see Suarez et al., 1995), small mammals in Cajas are not hunted for food. A number of indirect impacts, however, can be observed and anticipated, though not yet quantified. Agricultural activity occurs within the park. The impacts of ranching are of particular concern. In the páramo of Cajas, as elsewhere in Ecuador (Knapp, 1991), the graslands are grazed by cows and burning to provide fresh pasture is a regular occurrence (Huber, 1979; Ramsay and Oxley, 1996). For example, at Ventanas, a heavily grazed locality, no *Phyllotis* were caught. This was despite an abundance of rock outcrops in the close-cropped *pajonal*, of the kind normally favoured by this herbivorous rodent.

Burning results in loss of cover and food for rodents (Neal, 1970; Yates and Lee, 1997) and has been shown elsewhere to cause a temporary depression of rodent numbers and species diversity (e.g., Delany, 1986). Unless burning is so frequent as to cause habitat degradation, the impacts of such fires are usually temporary (Swanepoel, 1980; Kern, 1981; Rowe-Rowe and Lowry, 1982; Happold and Happold, 1989). Such perturbations are a common feature of high elevation habitats in the northern Andes (Armstrong and Macey, 1979; Lojtnant and Molau, 1982; Landázuri and Jijón, 1988; Lopez-Arevalo et al., 1993; Homewood, 1996), where humans have practiced fire-management of the region's grasslands for millennia (see Chapman, 1926; Knapp, 1991; Balslev and Luteyn, 1992; Homewood, 1996). Post-fire vegetation regeneration patterns reported by Ramsay and Oxley (1996) indicate that if the practices are operated at sustainable levels the effects on the Plateau's small mammal fauna may continue to be minimal at the meta-population level.

Quenoa forests are fragile ecosystems (Fjeldså and Kessler, 1996), and ranching activities may have severely impacted the quenoa forests of Cajas (Huber, 1979). Cows use them for shelter and in the process both trample the groundcover and destroy the natural windbreaks of *Diphlostegium* and *Gynoxis*. This causes desiccation and allows ingress of grassland plants. Both retard regeneration by *Polylepis* seedlings (see Smith, 1977) and together these three effects cause progressive loss of cover by this already localized habitat.<sup>30</sup> Five of Cajas' small mammal species appear to be restricted, or nearly so, to quenoa forest. Two (*M. altissimus* and *T. pyrrhonotus*) appear to favor degraded and/or disturbed forest, while *C. montivaga*, *T. cinnameus*, and *T. gracilis* are conspicuously absent from heavily disturbed forests, and will even be absent from those parts of an as-yet still closed-canopy quenoa forest that are most heavily visited by cows or humans. The third threat comes from tourism. Cajas is officially designated as a recreational area and the use of Cajas for such purposes has risen in the last few years (see Ashe

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<sup>30</sup> The extent of loss of *Polylepis* cover in Cajas can be gauged from the fact there are several place names that specifically mention this forest type (e.g., "Quinoascocha" - 'polylepis lake'), that now no longer have any such forest in their vicinity.

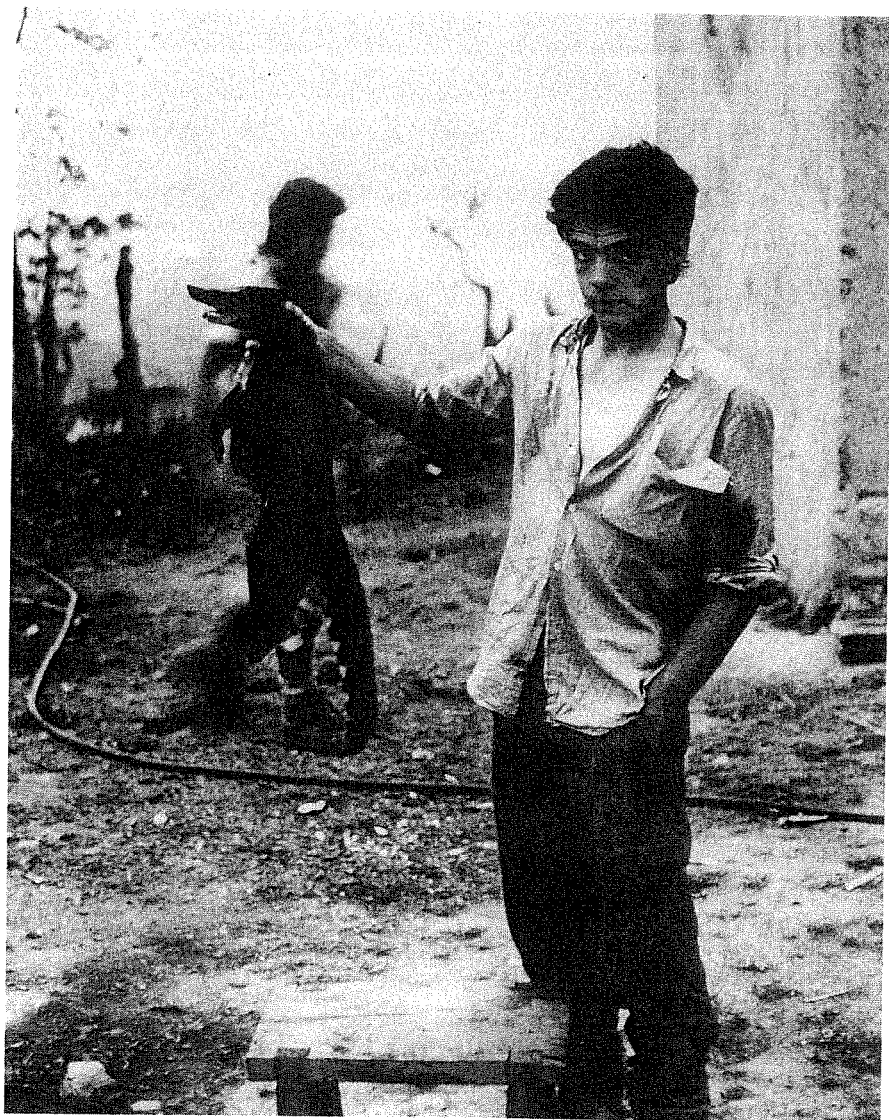


Figure 10. Fif Robinson with a mountain coati, *Nasua olivacea*; shot by hunters at Yakatuviana (2400m). Photograph, Adrian Barnett.

and Leschen, 1995; Barnett, 1997a). The effects of large numbers of humans to Cajas has not been quantified but such impacts are rarely positive for mammals (see Yalden, 1990; Gander and Ingold, 1997) or the vegetation cover on which they ultimately depend (e.g., Bayfield, 1980). The effects of trampling can be especially severe on moorland-like vegetation types, including páramo (see Brown et al., 1978; Bayfield and Brooks, 1979). The use of *Polylepis* for firewood at favored camp sites can have a very severe local impact (i.e., Lake Luspa) (see Huber, 1979). Littering and fecal pollution are collateral impacts of unexplored severity. Hunting of larger mammals (e.g., deer, *Odocoileus* and *Pudu*, and small carnivores like the mountain coati *Nasua olivacea*, see Fig. 10) and trapping for rabbits (*Sylvilagus brasiliensis*) have been observed during the study on several occasions. The lack of comparative data makes it difficult to assess the severity of these impacts, but it is suggested that a monitoring scheme be initiated.

### Other Mammal Species

Other mammals species recorded on the Cajas Plateau were: Andean Spectacled Bear (*Tremarctos ornatus*; páramo), Mountain Coati (*Nasua olivacea*; cloud forest), Weasel (*Mustela [frenata?]* cloud forest), Hog-nosed Skunk (*Conepatus chinga*; cloud forest), Mountain Lion (*Puma concolor*; páramo and cloud forest), Brocket Deer (*Mazama rufina*; cloud forest), White-tailed Deer (*Odocoileus virginianus*; cloud forest edges), Porcupine (*Coendou bicolor*; cloud forest), Mountain Guinea-pig (*Cavia porcellus*, páramo), and Rabbit (*Sylvilagus brasiliensis*, páramo and grassland in cloud forest zone). There were unconfirmed reports of Jaguarundi (*Felis yagouroundi*) and Northern Pudu (*Pudu mephistopheles*) at Mazán. Long-term residents reported the Andean fox (*Dusicyon culpaeus*) as formerly plentiful in the area, but now absent due to hunting pressure.

The following bats were recorded in the Rio Mazán valley by Fif Robinson (see Robinson and Hancock, 1986): *Anoura geoffroyi*, *Myotis* aff. *oxyotis*, *Sturnira erythromos*, *Histiotus montanus colombiae*, and *Desmodus rotundus*. *Myotis keaysi* was recorded nearby by LeVal (1973).

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## APPENDIX 1

## SYNONYMIES OF SPECIES KNOWN TO OCCUR ON THE CAJAS PLATEAU (\*) AND THOSE ECUADORIAN SPECIES MENTIONED IN THE TEXT (#).

SPECIES	SYNONYMIES
<i>Cryptotis montivaga</i> Anthony, 1921 <sup>1</sup> *	-
<i>Caenolestes caniventer</i> Anthony, 1921 *	-
<i>Caenolestes fuliginosus</i> (Tomes 1863) #	<i>centralis, obscura</i>
<i>Caenolestes tatei</i> Anthony, 1923 <sup>2</sup> *	-
<i>Akodon mollis</i> Thomas 1894 *	<i>altorum, fulvescens.</i>
<i>Akodon orophilus</i> Osgood, 1913 <sup>3</sup> *	-
<i>Anotomys leander</i> Thomas, 1906 #	-
<i>Chibchanomys orcesi</i> Jenkins and Barnett, 1997 *	-
<i>Ichthyomys hydrobates</i> Winge 1891 #	<i>nicefori, soderstromi.</i>
<i>Ichthyomys stolzmani</i> Thomas 1893 #	<i>orientalis.</i>
<i>Ichthyomys tweedii</i> Anthony, 1921 #	<i>caurinus.</i>
<i>Neusticomys monticolus</i> Anthony, 1921 #	-
<i>Microryzomys altissimus</i> (Osgood, 1933) *	<i>chotanus, hylaeus,</i> <i>Oryzomys altissimus.</i>
<i>Microryzomys minutus</i> (Tomes 1860) *	<i>dryas, fulvirostris, humilor,</i> <i>Oryzomys minutus</i>
<i>Oligorizomys destructor</i> (Tschudi 1844) *	<i>maranonicus, melanostoma, spodiurus, stolzmani.</i>
<i>Oryzomys albicularis</i> (Tomes 1860) *	<i>caracololus, childi, maculiventer, meridensis,</i> <i>oconnelli, pectoralis, perrensis.</i>
<i>Oryzomys auriventer</i> Thomas 1890 #	<i>nimbosus</i>
<i>Phyllotis andium</i> Thomas, 1912 *	<i>fruticolus, melianius, stenops, tamborum.</i>
<i>Phyllotis haggardi</i> Thomas, 1908 *	<i>elegantulus, fuscus.</i>
<i>Rhipidomys latimanus</i> (Tomes 1860) #	<i>colaensis, micotis, mollissimus, pictor.</i>
<i>Sigmodon inopinatus</i> Anthony, 1924 *	<i>hispidus.</i>
<i>Thomasomys aureus</i> (Tomes 1860) *	<i>altorum, nicefori, popayanus, preator, princeps.</i>
<i>Thomasomys baeops</i> (Thomas 1899) *	-
<i>Thomasomys cinnameus</i> Anthony, 1924 <sup>4</sup> *	<i>gracilis, hudsoni.</i>
<i>Thomasomys gracilis</i> Thomas, 1917 *	<i>cinnameus, hudsoni.</i>
<i>Thomasomys paramorium</i> Thomas 1898 *	-
<i>Thomasomys pyrrhonotus</i> Thomas 1886 *	<i>auricularis.</i>
<i>Thomasomys rhoadsi</i> Stone, 1914 #	<i>fumeus</i>
<i>Thomasomys silvestris</i> Anthony, 1914 #	-
<i>Aepomys lugens</i> (Thomas 1896) #	<i>otleyi, vulcani</i>

<sup>1</sup> According to Vivar et al. (1997), to be etymologically correct, the specific epithet should be '*montivagus*' so as to agree with the gender of the generic name, *Cryptotis*.

<sup>2</sup> Considered by Wilson and Reeder (1992) as a synonym of *Caenolestes fuliginosus*

<sup>3</sup> Formerly considered a sub-species of *A. mollis*, *A. orophilus* is now considered a valid species with two sub-species *A. o. orientalis* and *A. o. orophilus* (see Patton and Smith, 1992).

<sup>4</sup> *Thomasomys cinnameus* was listed as a synonym of *T. gracilis* by Wilson and Reeder (1992), but Robert Voss (pers. comm.) considers it to be a valid species. His opinion is followed here.

**Note:** When referring to earlier literature, it may be useful to first check the taxonomic histories compiled by G.H.H. Tate. These include *Phyllotis* (1932b), *Oryzomys* (*Oryzomys*) (1932c), *Oryzomys* (*Oligorizomys*, and others) (1932d), *Rhipidomys* and *Thomasomys* (1932e) and *Akodon* (1932f).

## APPENDIX 2

Collection numbers for skins collected by the author in Cajas and deposited in the collections of the Natural History Museum, London<sup>1</sup>

SPECIES /number of individuals	COLLECTION NUMBERS
<i>Cryptotis montivaga</i> Anthony, 1921 N = 9	84.385, 84.386, 84.387, 84.388, 84.389, 87.917, 87.918, 87.919, no number.
<i>Caenolestes caniventer</i> Anthony, 1921 N=1	84.383
<i>Caenolestes tatei</i> Anthony, 1923 N=1	84.384
<i>Akodon mollis</i> Thomas 1894 N=108	82.752, 82.755, 82.756, 82.759, 82.760; 82.761, 82.762, 82.763, 82.764, 82.765, 82.766, 82.767, 82.768, 82.769, 82.770; 82.771, 82.772, 82.773, 82.774, 82.775, 82.776, 82.777, 82.778, 82.779, 82.780; 82.781, 82.782, 82.783, 82.784, 82.785, 82.786, 82.787, 82.788, 82.789, 82.790; 82.791, 82.792, 82.793, 82.794, 82.795, 82.796, 82.797, 82.798, 82.799, 82.800; 82.801, 82.802, 82.803, 82.804, 82.805, 82.806, 82.807, 82.808, 82.809, 82.810; no number, 84.224, 84.225, 84.226, 84.232, 84.233, 84.234, 84.235, 84.236, 84.237, 84.238, 84.239, 84.240; 84.241, 84.242, 84.243, 84.244, 84.245, 84.246, 84.247, 84.248, 84.289, 84.250; 84.251, 84.252, 84.253, 84.254, 84.255, 84.256, 84.257, 84.258, 84.259, 84.260; 84.261, 84.262, 84.263, 84.264, 84.265, 84.266, 84.267, 84.268, 84.269, 84.270; 84.271, 84.272, 84.273, 84.274, 84.275, 84.276, 84.277, 84.278, 84.279, 84.280; 84.281, 84.282, 84.283, 84.284, 84.285, 84.286, 84.287, 84.288, 84.289, 84.294, 84.298, 85.882.
<i>Akodon orophilus</i> Osgood, 1913 N = 9	82.750; 82.753, 84.290; 84.291, 84.292, 84.293, 84.295, 84.296, 84.297.
<i>Chibchanomys orcesi</i> Jenkins and Barnett, 1997 N=3	82.815, 82.816, 84.349.
<i>Oligoromys destructor</i> (Tschudi 1844) N=5	82.847, 84.299, 84.300, 84.302, 84.303
<i>Oryzomys albigularis</i> (Tomes 1860) N=7	82.725, 82.726, 84.304, 84.305, 84.306, 84.307, 84.308.
<i>Microromys altissimus</i> (Osgood, 1933) N=27	82.829, 82.732, 82.733, 82.734, 82.735, 82.736, 82.739, 82.740; 82.741, 82.742, 82.743, 82.744, 82.745, 82.746, 82.747, 82.748, 82.749, 84.301, 84.309, 84.310 (twice), 84.312, 84.313, 84.314, 84.316, 84.317, 84.318.
<i>Microromys minutus</i> (Tomes 1860) N=2	82.731, 84.311
<i>Phyllotis andium</i> Thomas, 1912 N=1	82.813
<i>Phyllotis haggardi</i> Thomas, 1908 N=6	82.811, 82.812, 84.344, 84.345, 82.346, 82.347
<i>Sigmodon inopinatus</i> Anthony, 1924 N=4	82.814, 84.348, 85.884, 85.885
<i>Thomasomys aureus</i> (Tomes 1860) N=5	84.322, 84.323, 84.324, 82.325, no number
<i>Thomasomys baeops</i> (Thomas 1899) N=5	84.327, 84.330; 84.336, 84.337, 84.412.
<i>Thomasomys cinnameus</i> Anthony, 1924 N=6	84.315, 84.339, 84.340; 84.341, 84.342, 84.343,

<i>Thomasomys gracilis</i> Thomas, 1917 N=21	82.817, 82.818, 82.819, 82.820; 82.821, 82.822, 82.823, 82.824, 82.825, 82.826, 82.827, 82.828, 82.829, 82.830; 82.831, 82.832, 82.833, 82.834, 82.835, 82.837, 82.838.
<i>Thomasomys paramorum</i> Thomas 1898 N=13	82.839, 82.840; 82.841, 82.844, 82.845, 84.328, 84.329, 84.331, 84.332, 84.333, 84.334, 84.335, 84.338.
<i>Thomasomys pyrrhonotus</i> Thomas 1886	82.319, 82.320; 82.321, 82.842, 82.843

<sup>1</sup> The numbers in Appendix 2 refer only to skins. For some specimens only the skulls were preserved or accessed into the NHM collection. This accounts for the occasional mis-match between the numbers reported here and the species total numbers given in the text.







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