



Habitat Use and Ranging Behavior of *Callimico goeldii*

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Abstract We studied the diet, habitat use, and ranging behavior of 1 group of *Callimico goeldii* (callimicos) over 12 mo in northwestern Bolivia. The group's diet was comprised of fungi (39%), fruits (31%), arthropods (14%), exudates (14%), and other matter (2%). Callimicos concentrated their ranging activities in secondary forest (50%), primary forest with dense understory (30%), and bamboo (17%) habitats. The group's total home range was 114 ha; on average they used 38.4 ha/ mo and had a day range of 925 m. Monthly average day ranges—but not monthly home ranges—increased as frugivory declined, suggesting that subjects foraged on fungi and exudates by rechecking resources within a core area, making their day ranges longer than during months when they concentrated on fruit resources. The callimicos formed polyspecific associations with tamarins (*Saguinus labiatus* and *S. fuscicollis*) during 81% of observations. Day ranges increased in months with higher association rates which appears to result from the callimicos using a broader set of habitats when with tamarins than when alone. The ranging pattern of callimicos appears to be influenced primarily by 3 factors: their seasonal shift in diet requires that they forage in a variety of habitats across the year; their depletion of resources causes them to shift their core area over time; and their lack of territorial behavior eliminates the need to patrol boundaries as part of their daily movement. As a result, callimicos differ from many other callitrichids in their low ratio of day range length to home range size.

Keywords activity · callitrichids · day range · diet · height use · home range · polyspecific associations

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Introduction

Data on home range size and patterns of home range use are critical for understanding interactions among diet, ranging behavior, and territoriality in primates. A home range is the “area traversed by the individual in its normal activities of food gathering, mating, and caring for young” (Burt 1943, p. 351). The size and specific pattern of home range use of primate groups are influenced by many factors including group size and cohesion (Barton *et al.* 1992), seasonal changes in patch size and the distribution and availability of feeding sites (Clutton-Brock 1975; Harding 1976; Kaplin 2001; Olupot *et al.* 1997; Peres 1986; Soini 1993; Strier 1987), specific dietary requirements, the density and presence of neighboring groups, and intergroup social interactions including intrasexual tolerance (Isbell 1983; Garber 1988, 1993a). Daily path lengths, or the distance traveled in 1 day, are affected by similar factors, and among primates may also be influenced by the energetic costs of carrying large, dependent infants (Achenbach and Snowdon 2002; Digby and Barreto 1996).

We provide data on habitat use, home range use, and daily path lengths of Goeldi’s monkeys, *Callimico goeldii* (callimicos), inhabiting the western Amazon. *Callimico* is a monospecific genus, with only 1 species, *C. goeldii*, recognized in South America. Callimicos are members of the Callitrichidae, which also includes the marmosets (*Callithrix*, *Mico*, *Cebuella*, *Callibela*), lion tamarins (*Leontopithecus*), and tamarins (*Saguinus*). Callimicos, like the other callitrichids, are small-bodied (*ca.* 500 g) and have claw-like nails (tegulae; Porter and Garber 2004). Unlike the other callitrichids, and like all other platyrrhines, callimicos have single rather than twin births. Based on current genetic, morphological, and behavioral evidence, it appears that callimicos and marmosets are sister taxa (Chaves *et al.* 1999; Pastorini *et al.* 1998; Schneider and Rosenberger 1996; Singer *et al.* 2003; von Dornum and Ruvolo 1999), and that modern callimicos evolved single births from a marmoset ancestor that twinned (Porter and Garber 2004). The difference in litter size is likely to have a significant influence on the cost of infant care: callimico females have only a single infant that weighs *ca.* 8% of adult body mass at birth (Warneke 1992), whereas all other tamarins and marmosets produce infants whose combined mass at birth is 15–20% of adult body mass (Garber and Leigh 1997).

Given the proposed close evolutionary relationship between callimicos and marmosets, behavioral and anatomical differences between the taxa appear to reflect recent adaptations associated with the exploitation of different habitat types and resource conditions. Recent studies by Porter (2001a, b, c, 2004), Rehg (2003), Hanson (2000), Hanson *et al.* (2006), and Garber and Leigh (2001) have provided the first detailed behavioral and ecological data with which to assess the differences between callimicos and other callitrichids.

Porter (2001b) documented that fungi was a food resource regularly consumed by callimicos, comprising 29% of their yearly diet, and up to 63% of their diet during the dry season. The consumption of fungi—mycophagy—is common among some marsupials and rodents, but rare among primates (Hanson *et al.* 2003). Indeed, fungi appear to distinguish the callimico diet from that of sympatric callitrichids (*Saguinus fuscicollis*, *S. labiatus*, and *Cebuella pygmaea*), which rarely or never consume fungi (Porter 2001b; Soini 1988). Rehg (2003), following callimicos and tamarins at a study

site in Brazil, confirmed that fungi were an important component of the callimico diet, but found that fungi formed a smaller portion of total annual feeding time (19%).

In addition to dietary distinctions, patterns of home range use vary considerably between sympatric groups of tamarins and callimicos. Porter (2004) found that her study group of 6 callimicos occupied a home range of *ca.* 150 ha, about 5 times greater than similar-sized groups of sympatric tamarins. Hanson *et al.* (2006) proposed that the large home range of the callimicos resulted from the patchy distribution of fungi and a foraging pattern in which individuals reused fungal sites long term, allowing fungi to regrow where it had been previously harvested. However, Rehg (2003) found, over 9 mo, that her callimico study group concentrated its activities within a home range of only 59 ha. Our results allow us to propose factors that may account for the differences in the home range sizes among groups and across sites, which need to be evaluated with additional studies across the geographic range of *Callimico*.

In addition to fungi, callimicos consume fruit and arthropods, and to a lesser degree nectar, exudates, and invertebrates (Porter 2001b; Rehg 2003). Porter (2004) proposed that callimicos require a variety of microhabitats within their home ranges in which to find different food resources. They used primary forest with dense understory 76% of the time, and bamboo, secondary and stream edge habitats during 9%, 3% and 7% of the time, respectively. Rehg's (2003) study group was in primary forest with dense understory during 34% of observations and in bamboo habitats, including secondary bamboo and *taboca*, during 44% of observations. Short-term studies and surveys at other sites across the western Amazon basin indicated that callimicos might be bamboo and disturbed forest specialists (Buchanan-Smith 1991a; Ferrari *et al.* 1998; Izawa 1979) while others documented them in mature forests (Christen 1998; Christen 1999; Heltne *et al.* 1981). Thus, callimicos can tolerate a variety of habitat types, but researchers have limited information concerning the manner in which ranging patterns change across the habitats.

Despite dietary differences, callimicos and tamarins form mixed species troops. Callimicos form long-term polyspecific associations with sympatric species of tamarins including saddle-back tamarins (*Saguinus fuscicollis*), red-bellied tamarins (*S. labiatus*), and emperor tamarins (*S. imperator*) (Barry 2002; Porter 2001a; Rehg 2003). The associations are permanent at some sites, with 1 group of each species (callimicos, *Saguinus fuscicollis* and *S. labiatus*) coordinating their activities 61% of the time and sharing the same home range (Rehg 2003). At other sites, callimicos spend much of their time in association with tamarins (53%); however, they associate with several mixed-species tamarin groups rather than with 1 (Porter 2001a). Data from additional sites and groups will help to determine how polyspecific association patterns correspond with callimico ranging patterns.

In addition to differences in diet, differences in litter size between callimicos and other callitrichids likely influence ranging behavior, predation risk, and potentially infant survivorship. Carrying rapidly growing infants is energetically costly (Achenbach and Snowdon 2002); thus species with long day ranges likely face substantial costs associated with infant transport. Garber and Leigh (1997) reported that during the period of infant transport, *i.e.*, the first 3 months after birth, female callimicos have lower metabolic costs per litter, based on relative litter size growth trajectories, than

tamarins and marmosets that twins have when adjusted for maternal metabolic size. Thus, callimico ranging patterns may be less constrained by infant transport costs than those of twinning species of callitrichids.

We expanded our data base on callimico behavior and ecology by collecting data during a 12-mo field study of a new group of callimicos in Bolivia. We address the following questions: What are the day ranges and home ranges of callimicos, and how do they compare to those of other callitrichids? Do seasonal changes in diet influence habitat use and daily ranging patterns? Do polyspecific associations influence ranging patterns? Finally, what do the new data tell us about the habitat requirements of callimicos?

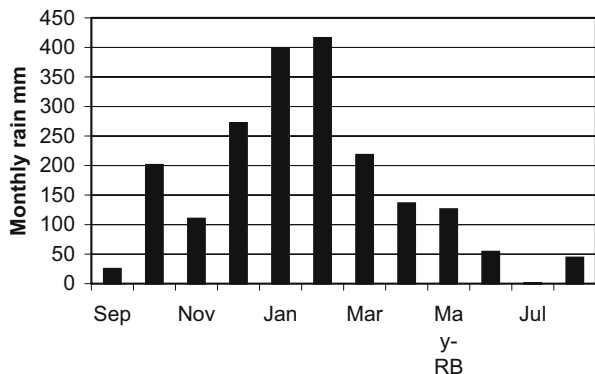
Methods

Study Site

We conducted research in northern Bolivia, in the Department of the Pando, at a field camp Callimico (UTM Zone 19, 0498129 W, 8737913 S, ca. 280 m a.s.l.), 1 km from the Tahuamanu Biological Field Station (formerly known as San Sebastian: Porter 2001b), 2 km north of the Río Tahuamanu, 42 km east of the border of Perú, and 52 km southwest of Cobija, the capitol of the Pando (Porter 2001b). The forest is representative of sandy-clay forests of the south and south-western Amazon Basin (Alverson *et al.* 2000), with pronounced dry and rainy seasons. In previous study years, Porter (2001b) defined the wet season as November–April, and the dry season as May–October. For consistency, we use the same time periods, though during our study rainfall was greater in October than in either November or April (Fig. 1). Total rainfall for September 2002–August 2003 was 2001 mm.

The forest around Camp Callimico had been selectively logged for mahogany (*Swietenia macrophylla*), Spanish cedar (*Cedrela odorata*), and palm trees (*Euterpe precatoria*) 3–7 years earlier. There are small (1 ha) patches of secondary forest at the site of an abandoned house and 3 abandoned agricultural plots, and an additional

Fig. 1 Mean monthly rainfall (mm) throughout the study period in Cobija, Pando (NOAA 2002, 2003). Because data were unavailable for May and June, we used data from the next nearest NOAA source, Rio Branco, Acre, Brazil (RB) for May and June as an approximate measure for Cobija.



7 ha of forest has been cleared for agriculture and pasture (Fig. 2). Humans collect Brazil nuts in the forest each year from January through April. Beginning in March, we cut a new set of trails to augment the trail system established at the Field Station in 1997 (Porter 2001b). We established trails at 100-m intervals north-south and east-west forming a grid of 1-ha plots. In areas of dense forest, we cut additional trails at 50-m intervals to facilitate observations.

Study Group

We habituated callimicos from March to August, 2002. In September, we followed the group, but could not consistently collect data because the subjects remained shy. Thus, we report only data on day range distances and home range size for September, and no datum on other behaviors. From October through mid-November 2002, we collected focal individual samples; however, we could not consistently identify all individuals and samples may not be balanced among all group members. From mid-November 2002 through August 2003, we consistently identified individuals; therefore, we followed a different group member each day to provide an equal number of observation days of each group member per month. We collected data on focal individuals via point samples (Martin and Bateson 1993) at 5-min intervals from the time the individual left its sleeping site in the morning until

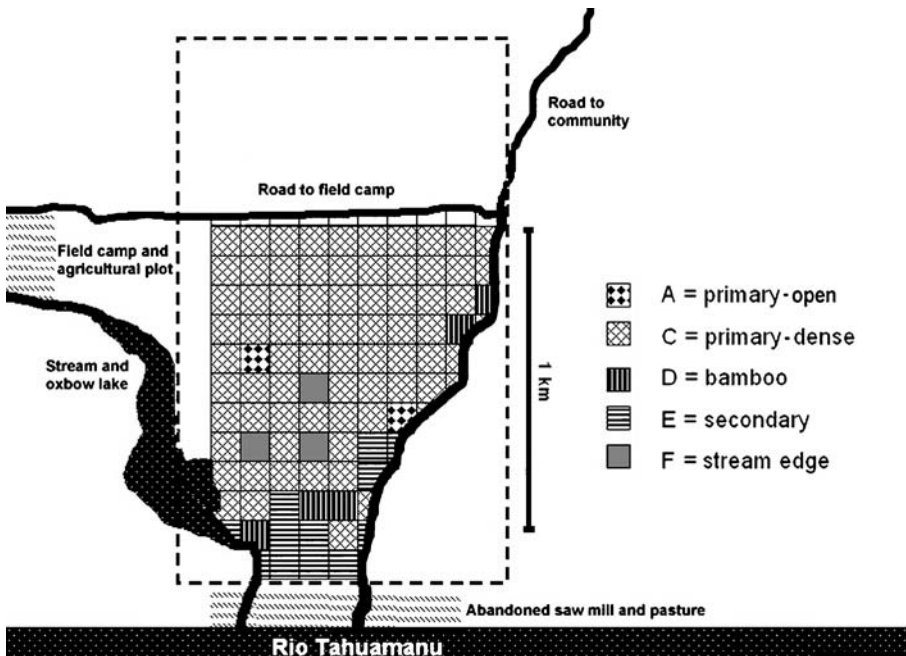


Fig. 2 Research area indicating landmarks and distribution of habitat types. The dotted square indicates the area shown in Figs. 7 and 8, and contained a grid trail system with trails oriented north-south and east-west at 100-m intervals.

it retired to its sleeping site at night. On some days, observation times were shorter owing to loss of the group, torrential rain, or other factors. We also noted infant transport during months in which the group contained dependent young, i.e., infants transported by adults. We did not collect data during February, 2003. In total, we collected 1375 observation hours (Table I).

We recorded the following data on the focal individuals during observations: their activity (resting, traveling, eating, foraging), if eating the type of food being eaten, the height class and habitat type they occupied, and their location in the trail system. We noted food types using the following categories: fungus, nectar, fruit, plant exudate, arthropod, and vertebrate. We used the following height classes to define vertical distance from the forest floor to the focal individual (Porter 2004): 0, 0 m; 1, >0–5 m; 2, >5–10 m; 3, >10–15 m; 4, >15–25 m; and 5, \geq 25 m. We also recorded the habitat type that the focal individual occupied via a coded system for microhabitats (Porter 2004) based on the height of canopy, visibility criteria, and the dominant plant species present in a 10 m³ cube around the focal individual. We determined visibility by noting the maximum observable distance at eye level at which we could potentially see a subject. We defined habitats via the following criteria: primary forest with open understory = primary forest, canopy >15 m, visibility at eye level >20 m; primary forest with dense understory or maturing secondary forest = canopy >15 m, visibility at eye level <20 m; bamboo forest = bamboo dominant plant species, canopy <15 m, visibility at eye level < 20 m; secondary forest = discontinuous canopy with the majority of trees <15 m, visibility <20 m; stream edge forest = streams edge habitat, canopy >15 m, visibility <20 m, dominant plants ferns and stilt root palms. We estimated habitat availability by recording the habitat at 100-m intervals along all north-south trails, at 102 points.

Table I Monthly activity budget of *Callimicos*

| Month | Observation hours | Forage | | Eat | | Rest | | Travel | | Other | |
|-------------------|-------------------|--------|----------|-----|----------|------|----------|--------|----------|-------|----------|
| | | % | <i>N</i> | % | <i>N</i> | % | <i>N</i> | % | <i>N</i> | % | <i>N</i> |
| September | 55 ^a | | | | | | | | | | |
| October | 108 | 8 | 106 | 8 | 108 | 49 | 648 | 29 | 375 | 5 | 62 |
| <i>November</i> | 212 | 6 | 78 | 5 | 64 | 50 | 700 | 37 | 518 | 3 | 37 |
| <i>December</i> | 132 | 2 | 17 | 9 | 83 | 45 | 435 | 43 | 414 | 1 | 9 |
| <i>January</i> | 113 | 6 | 85 | 7 | 103 | 46 | 680 | 40 | 594 | 2 | 31 |
| <i>March</i> | 141 | 4 | 40 | 9 | 103 | 50 | 558 | 35 | 391 | 3 | 30 |
| <i>April</i> | 72 | 5 | 71 | 12 | 173 | 47 | 699 | 35 | 513 | 1 | 21 |
| May | 121 | 3 | 72 | 10 | 250 | 57 | 1444 | 30 | 747 | 0 | 3 |
| June | 95 | 2 | 30 | 5 | 86 | 66 | 1096 | 27 | 445 | 0 | 5 |
| July | 121 | 2 | 44 | 6 | 157 | 65 | 1699 | 28 | 727 | 0 | 4 |
| August | 205 | 2 | 29 | 5 | 83 | 62 | 968 | 30 | 445 | 0 | 1 |
| Dry season | 650 | 3 | | 7 | | 61 | | 29 | | 1 | |
| <i>Wet season</i> | 670 | 5 | | 8 | | 48 | | 38 | | 2 | |
| Total | 1375 | 4 | | 8 | | 55 | | 32 | | 1 | |

Wet season months are in italics.

^aData treated separately; see text for explanation.

Because callimico group members travel cohesively (average distance between group members is <3.5 m (Porter 2003; Porter and Garber *in press*), location data collected for 1 group member are the same as for the whole group. We recorded location data by noting the coordinates of the nearest east-west and north-south trails that formed the 1-ha plot grid the focal individual occupied. We subsumed location data from 0.25-ha plots within the 1-ha plot in which they were positioned.

We scored interspecific associations, including both physical proximity (an individual of a tamarin species was <25 m from focal individual) and vocal contact (tamarins and callimicos were in vocal contact), during each 5-min scan. Thus polyspecific associations represent the number of intervals in which 2 groups were <25 m of each other, or in vocal contact. The use of 1:0 sampling should not overestimate association duration (Martin and Bateson 1993) because the sample interval used—5 min—was much shorter than the typical association, which was generally long-lasting and uninterrupted. The protocol is the same as Porter's (2001a) except that the proximity criterion by which we considered the 2 species to be associated was <25 m instead of 15 m. The change allowed us to count individuals that were in the same tree but at different levels (understory vs. canopy) as in association.

Analyses

We calculated home range size by counting the total number of 1-ha quadrats that the study group entered. The method provides a maximum estimate of home range size. For each study month, we counted the total number of times individuals used a quadrat and then converted the number into a percentage based on the total number of samples taken that month. We calculated day range from 10 d/mo, except for September ($n=5$), December ($n=6$), and March ($n=9$). On each day we collected ≥ 8 h of observations. Because we did not directly measure path length, we multiplied the average number of quadrats used per day by the width of a quadrat (100 m) to provide a rough estimate of daily path length. In addition, if the group left a quadrat that it returned to later in the day, we counted the quadrat again for the day range calculations.

We summed all feeding records during each study month and converted them into a percentage to represent the proportion of the monthly activity budget devoted to exploiting each food type. In the analyses, we included no record of eating for which the food item was not noted or was unknown: the unknown records account for 27% of all feeding observations. We may have introduced some bias into our dietary calculations by excluding the unknown data if a particular food type was consistently missed; however, we assume that we missed equal numbers of all food types. We counted habitat and height data for each month to determine the percentage of time that subjects used each habitat and each height class. We used χ^2 tests for independence to determine whether callimico diet, microhabitat use, and height class use varied between the wet and dry season.

We conducted 2-tailed Spearman rank correlations to test whether diet, habitat, height, polyspecific association status, day range, and home range correlate with one another. In all analyses $p=0.05$.

Results

Size and Composition of the Study Group

The callimico group contained 1 adult female, 2 adult males, and 1 infant female born *ca.* August 20, just before the start of data collection. The adult female nursed her offspring until December, when nursing/nipple contact ceased (Porter and Garber *in press*). All adults helped to transport and to provide food—fungi, fruits, and arthropod—to the young female. Both males mated with the female, indicating that the group was characterized by a polyandrous mating pattern (Porter and Garber *in press*). Although we believed the adult female was pregnant, due to her increasing weight in December and January, we observed no new infant.

Activity Budget

The monthly activity budget is in Table I. It varied significantly between the wet and dry seasons ($\chi^2 > 33.37$, $p < 0.001$, $df = 4$). Resting increased from 48% in the wet season to 61% in the dry season. Correspondingly, travel decreased in the dry season (38% wet season vs. 29% dry season). Other activities remained relatively constant between seasons. Feeding included only periods when individuals consumed food. Foraging included only periods during which individuals actively searched for or manipulated food. Stationary callimicos commonly visually scan the environment, possibly to locate insects or understory fruits, conspecifics, or detect potential predators, which we recorded as resting. Thus, our foraging rates represent minimum values.

Diet

Based on monthly feeding data, fungi were the most common food items in the callimico diet (39% of diet), followed by fruits (31%), arthropods (14%), exudates (14%), and other items, e.g., vertebrates and dirt (2%). Diet changed across the study months (Table II) and is significantly different in the dry and wet season ($\chi^2 > 33.37$, $p < 0.001$, $df = 4$). Individuals consumed fungi and exudates more in the dry season than in the wet season and fruits more in the wet season than in the dry season. In contrast, subjects ate arthropods consistently across seasons. However, dietary pattern varies considerably between months during the same season. For example, fruits account for 88% of feeding time in November and only 59% of feeding time in December, both wet season months. Similarly, fungi comprise 62% of callimico feeding time in the dry season month of June, but only 42% of feeding time in the dry season month of July (Table II).

Habitat Use

Callimicos use secondary forest habitats most frequently across the year (50% of observations), followed by primary forest with dense understory and maturing secondary forest (30%), bamboo forest (17%), primary forest with open understory (2%), and stream edge forest (1%). Habitat use varies significantly by season

Table II Dietary profile of *Callimicos*

| Time period | Fruit | | Fungi | | Arthropods | | Exudates | | Other | |
|-------------------|-------|----------|-------|----------|------------|----------|----------|----------|-------|----------|
| | % | <i>N</i> | % | <i>N</i> | % | <i>N</i> | % | <i>N</i> | % | <i>N</i> |
| October | 65 | 37 | 5 | 3 | 19 | 11 | 0 | 0 | 11 | 6 |
| <i>November</i> | 88 | 23 | 4 | 1 | 8 | 2 | 0 | 0 | 0 | 0 |
| <i>December</i> | 59 | 20 | 41 | 14 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>January</i> | 42 | 21 | 18 | 9 | 28 | 14 | 0 | 0 | 12 | 6 |
| <i>March</i> | 66 | 50 | 17 | 13 | 13 | 10 | 3 | 2 | 1 | 1 |
| <i>April</i> | 43 | 59 | 33 | 46 | 17 | 24 | 5 | 7 | 1 | 2 |
| May | 21 | 45 | 57 | 122 | 7 | 16 | 13 | 27 | 2 | 4 |
| June | 8 | 7 | 62 | 53 | 9 | 8 | 20 | 17 | 0 | 0 |
| July | 8 | 11 | 42 | 58 | 18 | 24 | 29 | 40 | 3 | 4 |
| August | 6 | 5 | 30 | 25 | 21 | 17 | 39 | 32 | 4 | 3 |
| Dry season | 19 | 105 | 46 | 261 | 13 | 76 | 21 | 116 | 1 | 8 |
| <i>Wet season</i> | 54 | 173 | 26 | 83 | 16 | 50 | 3 | 9 | 1 | 5 |
| Total | 31 | 278 | 39 | 344 | 14 | 126 | 14 | 125 | 2 | 13 |

Food items are expressed as a % of the total monthly records and as the actual no. of feeding records. Wet season months are in italics.

(Table III: $\chi^2 > 16.26$, $p < 0.001$, $df = 3$): subjects use primary forest with dense understory more in the wet season than in the dry season (49% vs. 17% respectively), and secondary forest more in the dry season than the wet season (62% vs. 32% respectively). In addition, habitats are not used in proportion to their abundance ($\chi^2 > 16.26$, $p < 0.001$, $df = 3$), e.g., although primary forest with dense understory forms ca. 74% of the total available habitat, callimicos used it only 30% of the time (Table III).

Table III Monthly habitat use data expressed as a % of the monthly records and as the actual no. of habitat records

| Time period | Primary open understory (A) | | Primary dense understory (C) | | Bamboo (D) | | Secondary forest (E) | | Streams edge (F) | |
|-------------------|-----------------------------|----------|------------------------------|----------|------------|----------|----------------------|----------|------------------|----------|
| | % | <i>N</i> | % | <i>N</i> | % | <i>N</i> | % | <i>N</i> | % | <i>N</i> |
| October | 2 | 29 | 58 | 707 | 14 | 173 | 19 | 234 | 7 | 84 |
| <i>November</i> | 0 | 2 | 74 | 1020 | 20 | 273 | 5 | 62 | 1 | 20 |
| <i>December</i> | 1 | 12 | 59 | 570 | 28 | 270 | 12 | 110 | 0 | 0 |
| <i>January</i> | 3 | 37 | 53 | 789 | 11 | 170 | 33 | 491 | 0 | 0 |
| <i>March</i> | 1 | 14 | 32 | 365 | 8 | 85 | 59 | 662 | 0 | 0 |
| <i>April</i> | 5 | 70 | 28 | 415 | 15 | 212 | 51 | 754 | 1 | 21 |
| May | 1 | 25 | 16 | 396 | 19 | 478 | 64 | 1621 | 0 | 11 |
| June | 1 | 12 | 5 | 89 | 18 | 297 | 76 | 1267 | 0 | 4 |
| July | 2 | 59 | 11 | 300 | 16 | 413 | 70 | 1853 | 1 | 17 |
| August | 5 | 86 | 10 | 150 | 20 | 321 | 64 | 1020 | 1 | 10 |
| Dry season | 2 | 211 | 17 | 1642 | 17 | 1628 | 62 | 5995 | 1 | 126 |
| <i>Wet season</i> | 2 | 135 | 49 | 3159 | 16 | 2079 | 32 | 2079 | 0 | 21 |
| Total use | 2 | 346 | 30 | 4801 | 17 | 2692 | 50 | 8074 | 1 | 147 |
| Available | 2 | 2 | 74 | 76 | 5 | 5 | 16 | 16 | 3 | 3 |

Wet season months are in italics.

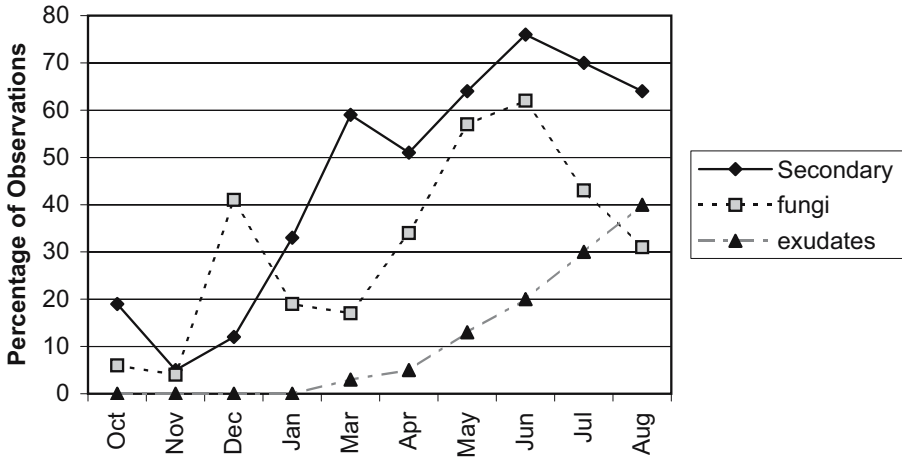


Fig. 3 Percentage of observations spent in secondary forest plotted with the percentages of fungi and exudates in the monthly diet.

There are significant positive correlations between monthly averages of secondary forest (habitat E) use and the percentage of fungi and exudates in the diet (Fig. 3; $r=0.723$, $p<0.05$, $r=.891$, $p<0.01$, respectively). Similarly, there are significant positive correlations between primary forest with dense understory (habitat C) use and the percentage of fruit in the diet ($r=.918$, $p<0.01$; Fig. 4).

Although the resources callimicos exploit are present in all habitat types, individuals consume fruits, fungi, arthropods, and exudates in different frequencies among habitat types across the year ($\chi^2>44.81$, $p<0.001$, $df=9$; Fig. 5). However, they consume all food types except fruits most frequently in secondary forest.

Height Class Use

Callimicos fed, foraged, rested, and traveled at all heights throughout the forest canopy including the ground (Table IV). However, when expressed as a percentage

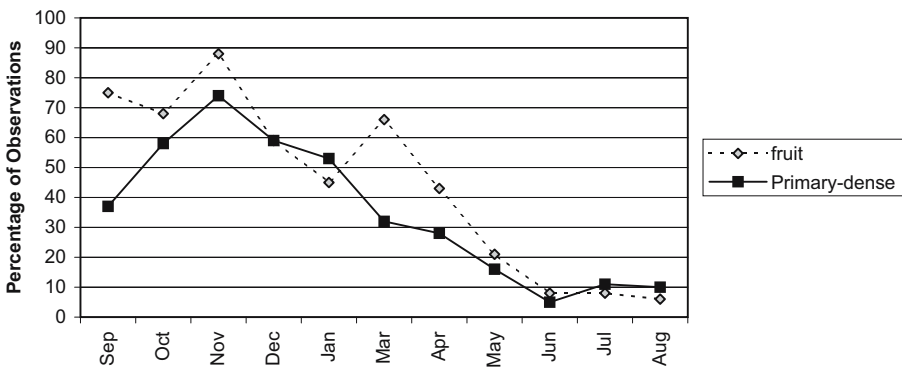


Fig. 4 Percentage of observations in primary forest with dense understory plotted with the percentage of fruit in the monthly diet.

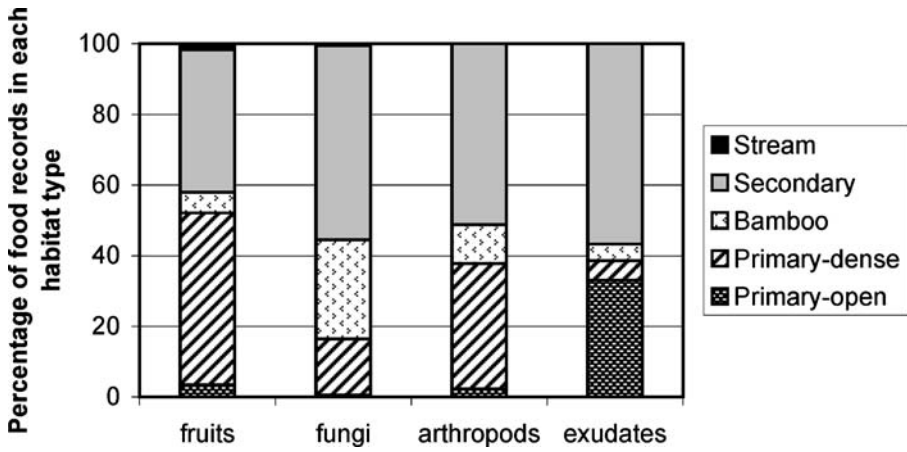


Fig. 5 Percentage of records that foods were eaten in different habitat types during all study months.

of total observation time, 94% of the callimico activity budget occurs 0–5 m above the ground and <2% of activity occurs at >10 m. Callimicos use higher levels of the canopy in the wet season (7% of activity >5 m) than in the dry season (3% of activity >5 m) ($\chi^2 > 26.85, p < 0.001, df = 4$); however, in general callimicos travel and feed in the understory throughout the entire year.

Polyspecific Associations

Callimicos associated regularly with 3 different groups of tamarins. In total, the callimico group was alone during 19% of observations, in vocal contact with tamarins during 1% of observations, and in proximity to them during 80% of observations. There were minimal seasonal differences in association rates by

Table IV Monthly height use data expressed as a % of monthly records and as the actual # of records in each height class

| Time period | Ground | | 0–5 m | | 5–10 m | | 10–15 m | | 15–25 m | |
|-------------|--------|-----|-------|-------|--------|-----|---------|-----|---------|-----|
| | % | N | % | N | % | N | % | N | % | N |
| October | 0 | 4 | 89 | 1122 | 8 | 101 | 2 | 22 | 1 | 9 |
| November | 0 | 1 | 90 | 1232 | 6 | 82 | 2 | 33 | 2 | 27 |
| December | 0 | 3 | 93 | 891 | 3 | 32 | 3 | 23 | 1 | 12 |
| January | 1 | 21 | 92 | 1369 | 5 | 68 | 2 | 26 | 0 | 3 |
| March | 0 | 3 | 94 | 1055 | 3 | 34 | 3 | 3 | 0 | 3 |
| April | 1 | 12 | 90 | 1332 | 4 | 61 | 1 | 15 | 4 | 50 |
| May | 0 | 5 | 95 | 2412 | 2 | 46 | 3 | 61 | 0 | 4 |
| June | 0 | 0 | 99 | 1659 | 1 | 10 | 0 | 0 | 0 | 0 |
| July | 1 | 14 | 99 | 2611 | 0 | 3 | 0 | 13 | 0 | 0 |
| August | 3 | 46 | 96 | 1522 | 1 | 18 | 0 | 1 | 0 | 0 |
| Dry season | 1 | 69 | 96 | 9326 | 2 | 178 | 1 | 97 | 0 | 13 |
| Wet season | 1 | 40 | 92 | 5879 | 4 | 277 | 2 | 129 | 1 | 95 |
| Total | 1 | 109 | 94 | 15205 | 3 | 455 | 1 | 226 | 1 | 108 |

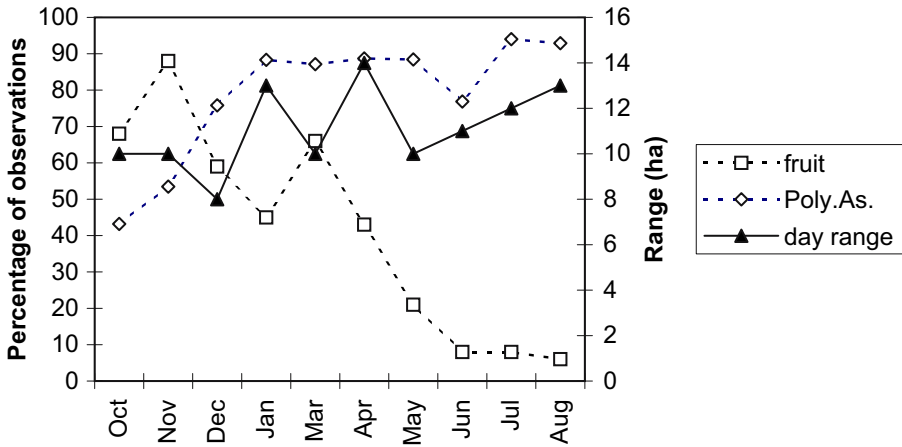


Fig. 6 Percentage of monthly observations spent in polyspecific associations and monthly percentage of fruit in the diet, plotted with mean monthly day ranges (ha).

season: during wet season months associations occurred during 80% of observations, and during dry season months they occurred during 82% of observations. The percentage of time in physical association varied across study months (Fig. 6), with the lowest frequency of association during October and November.

Home Range

Callimicos exploited an area of 114 ha (Table V, Fig. 7a). The monthly average number of hectares used was 38.4 ha, with a maximum of 55 ha exploited in October (Fig. 7b), and a minimum of 27 ha exploited in December (Fig. 7c). Home range sizes do not correlate with the percentage of the monthly activity budget spent resting, traveling, foraging, eating, foraging combined with eating, or with food type, habitat use, or time spent in polyspecific associations. Although the specific area

Table V Monthly home range and mean day range values

| Time period | Home range (ha) | Day range (ha) ± SD |
|----------------|-----------------|---------------------|
| September | 34 | 7.0±2.9 |
| October | 55 | 8.7±3.9 |
| November | 31 | 8.5±4.5 |
| December | 27 | 7.3±3.1 |
| January | 47 | 9.9±2.9 |
| March | 31 | 8.6±1.2 |
| April | 38 | 10.2±2.6 |
| May | 38 | 9.5±2.7 |
| June | 49 | 8.6±4.6 |
| July | 42 | 9.6±2.4 |
| August | 28 | 10.7±2.8 |
| Dry season | 40.6 | 9.4±3.2 |
| Wet season | 34.8 | 9.1±3.2 |
| Yearly average | 38.4 | 9.25±3.2 |

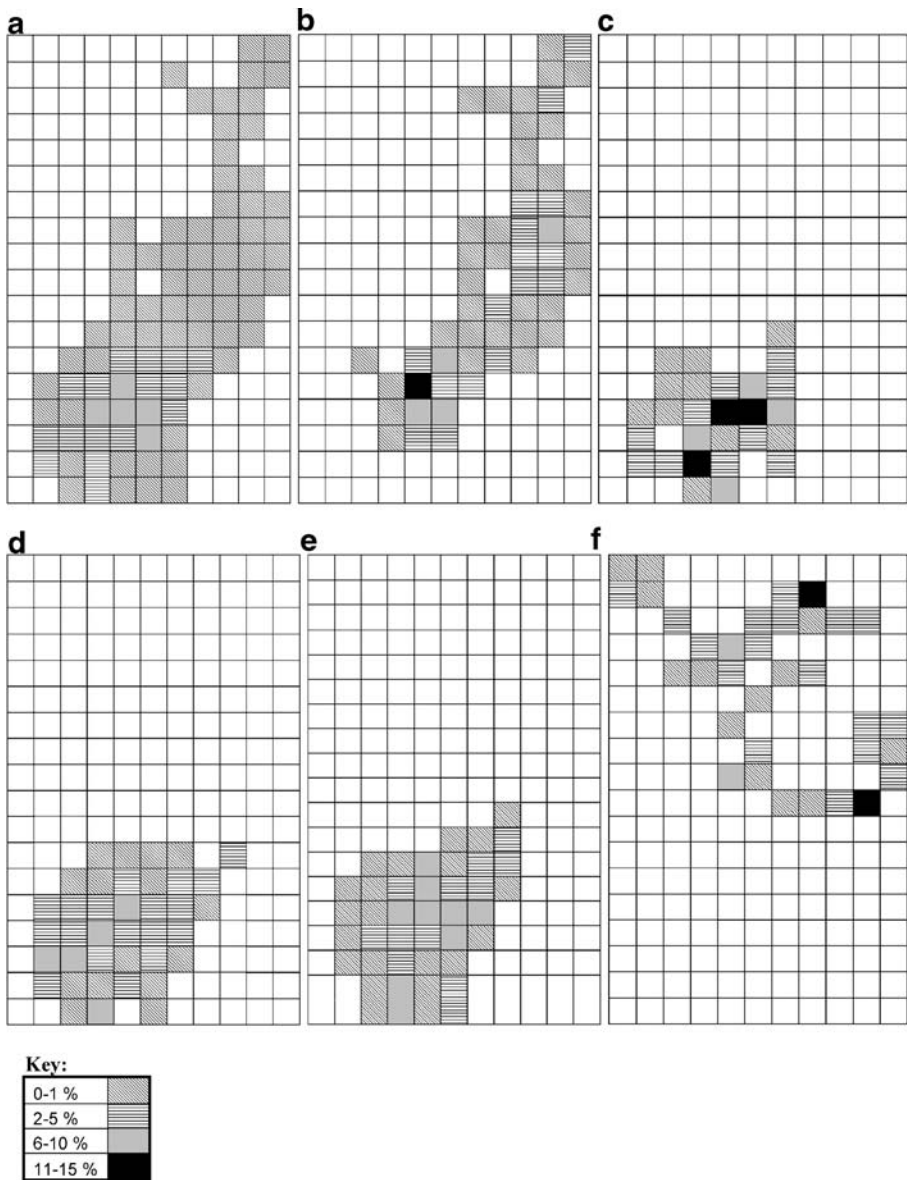


Fig. 7 Home range use (a) across the study (October 2002–August 2003); (b) in October; (c) in December; (d) in April; (e) in May; (f) in September.

used each month varied across the study, some months, such as April and May, showed very similar home range use patterns (Fig. 7d,e).

In September, the group spent the majority of time in the northern part of its range (Fig. 7f). They crossed into the northern part of the grid several times before the project began; thus use of the area in September was not due to abnormal ranging during the habituation process. In October, callimicos also used parts of the northern

section of the grid, but did not enter them thereafter. In total, the callimicos used 71 ha in September and October (62% of total range), whereas the rest of the year they used 67 ha (59% of total range).

Figure 8 contains home range use as it corresponds with monthly activities (excluding September) including resting (8a), traveling (8b), and foraging combined with eating (8c). Quadrats that contained sleeping sites are in Fig. 8a, along with the percentage of nights individuals used that quadrat for sleeping. The locations of encounters on 2 different days with an extragroup male are in Fig. 8b. Thus, despite having a large home range, callimicos use a small set of quadrats intensively and travel through or exploit other quadrats rarely or extremely seasonally. The number of hectares used in the dry season (40.6) is larger than the number used in the wet season (34.8).

Day Range

The monthly means of the number of quadrats entered per day are in Table V. On average the group entered 9.25 ha/d (including revisits to a quadrat that they had previously used), but day range varies considerably from a minimum of 2 ha to a maximum of 20 ha. The estimates do not include the distance covered during circular movements within a given hectare. A rough estimate of daily path in meters can be calculated by multiplying the number of hectares entered by 100 m; thus the mean day

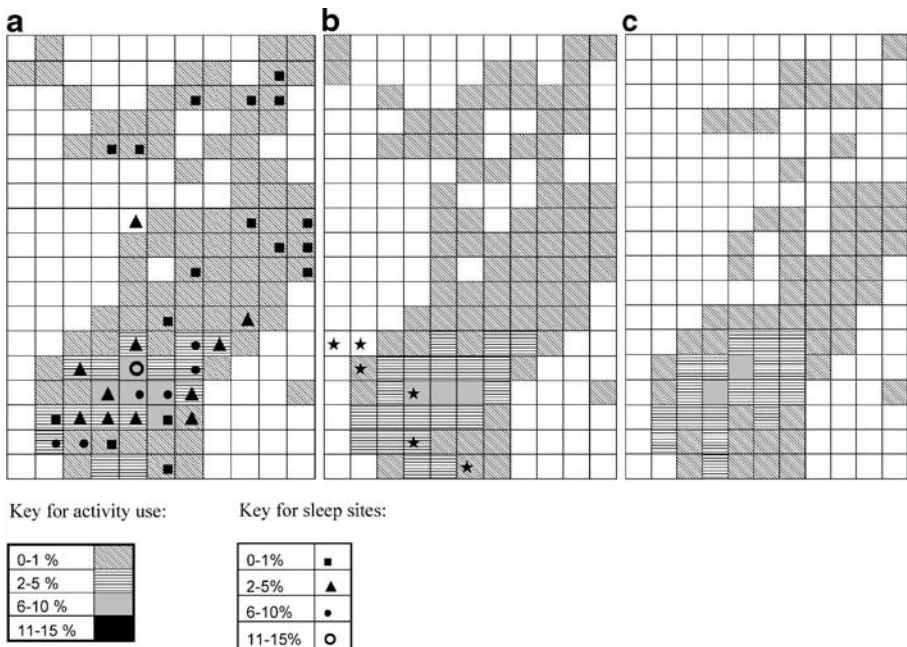


Fig. 8 Percentage of observations that quadrats were used for activities (a) rest; (b) travel; and (c) forage and eat. The percentages of nights that subjects used quadrats as sleeping sites are indicated in Fig. 7a with symbols. The locations of encounters with a non-group male are indicated in Fig. 7b with stars.

range was 925 m/d. Mean day range was only slightly greater during the dry season (9.4 ha) than in the wet season (9.1 ha).

There is no significant correlation between monthly home range values and monthly frequencies of mycophagy, insectivory, gummivory, or microhabitat use. When monthly average day range values are compared to the same variables, there is a negative correlation between monthly average day range and frugivory (Fig. 6; $r = -.661$, $p < 0.05$): as frugivory decreased, day range increased. In addition, monthly day ranges correlate positively with polyspecific association rates: months with higher polyspecific association rates are also those with longer day ranges (Fig. 6).

Discussion

Our results along with those of Rehg (*in press*) provide the first opportunity to compare callimico ranging behavior with those of other primates. Home range size and day range lengths vary considerably among the callitrichids, with marked specific differences across sites and taxa (Table VI). Determining the factors responsible for the variation is important for understanding specific solutions to ecological problems associated with exploiting resources, avoiding predators, and defending territories. The information is also essential to develop conservation strategies appropriate for callimicos because it provides data needed to determine the size and habitat required to sustain callimico groups. We outline several ecological factors that appear to influence callimico ranging behavior, with the goal of promoting additional studies of callimico ecology at other sites and study groups.

Group size is one factor that researchers suggested influences home range size in primates (Chapman and Chapman 2000). As the size of a primate group increases, both scramble competition and contest competition may increase, resulting in group members traveling greater distances and exploiting a greater number of feeding sites to obtain a constant or adequate diet (Chapman and Chapman 2000; Janson and Goldsmith 1995). However, empirical data on smaller and larger groups of the same species have generally failed to support this theoretical contention (Sussman and Garber 2004, 2007).

Although Dietz *et al.* (1997) reported that in golden-lion tamarins home range and day range size correlates strongly with group biomass, it does not appear to be the case for many other callitrichid taxa (Table VI). In a study of 101 groups and 27 species of callitrichids, owl monkeys, and titi monkeys, Peres (2000, p. 113) found that “greater group biomass did not necessarily result in commensurately larger home ranges.” In our study, the callimico group of 4 individuals had a home range of 114 ha, whereas at the same site a different group of 3–7 callimicos (group size varied during the study) inhabited a larger home range of 150 ha (Porter, 2001). Further, a group of 7–9 callimico in Brazil had a home range of just 59 ha (Rehg, *in press*). Thus, group biomass does not appear to explain differences in the size of home ranges of different callimico groups or of callimicos versus other callitrichids.

However, determining the degree to which group size affects foraging and ranging patterns for callimicos and other callitrichids is complicated by their tendency to

Table VI Comparison of home range size, day range length, and biomass for groups of various callitrichids

| Genus | Species | Ave. body mass (kg) ^a | Ave. home range (ha) | Ave. day range (m) | Ave. group size | Group biomass ^b (kg/km ²) | Reference |
|--------------------------|--------------------|----------------------------------|----------------------|--------------------|-----------------|--|----------------------------|
| <i>Callimico</i> | <i>goeldii</i> | .525 | 114 | 925 | 4 | 1.5 | This article |
| <i>Callimico</i> | <i>goeldii</i> | .525 | 150 | — | 4.5 | 1.3 | Porter 2001a |
| <i>Callimico</i> | <i>goeldii</i> | .525 | 59 | — | 8 | 5.2 | Rehg, in press |
| <i>Cebuella</i> | <i>pygmaea</i> | .120 | 0.5 | 290 | 6.5 | 129.9 | Soimi 1988 |
| <i>Callithrix</i> | <i>aurita</i> | .429 | 35.3 | 958 | 8.5 | 8.6 | Correa 1995 |
| <i>Callithrix</i> | <i>flaviceps</i> | .406 | 35.5 | 1222 | 13 | 12.4 | Ferrari 1988 |
| <i>Callithrix (Mico)</i> | <i>humeralifer</i> | .475 | 28 | 1459 | 11.5 | 16.2 | Rylands 1982 |
| <i>Callithrix</i> | <i>jacchus</i> | .320 | 0.5 | 200 | 11 | 586.1 | Stevenson and Rylands 1988 |
| <i>Callithrix</i> | <i>jacchus</i> | .320 | 1.2 | 1010 | 5 | 111 | Hubrecht 1984 |
| <i>Callithrix</i> | <i>jacchus</i> | .320 | 5.2 | 912 | 7 | 35.9 | Digby and Barreto 1995 |
| <i>Callithrix</i> | <i>jacchus</i> | .320 | 4.6 | 1181 | 13 | 75.3 | Digby and Barreto 1995 |
| <i>Callithrix</i> | <i>jacchus</i> | .320 | 3.9 | 1243 | 12 | 82 | Digby and Barreto 1995 |
| <i>Callithrix</i> | <i>kuhli</i> | .375 | 10 | 942 | 6.6 | 20.6 | Rylands 1982 |
| <i>Saguinus</i> | <i>fuscicollis</i> | .350 | 30 | 1220 | 5 | 4.9 | Terborgh 1983 |
| <i>Saguinus</i> | <i>fuscicollis</i> | .350 | 40 | 1849 | 7.5 | 5.5 | Garber, 1993 |
| <i>Saguinus</i> | <i>fuscicollis</i> | .350 | 154 | 1991 | 6.5 | 1.23 | Peres 1992a |
| <i>Saguinus</i> | <i>geoffroyi</i> | .497 | 26 | 2061 | 6.1 | 9.7 | Dawson 1975, 1978 |

| | | | | | | |
|-----------------------------------|------|------|------|-----|-------|-----------------------------|
| <i>Saguinus imperator</i> | .475 | 30 | 1420 | 4 | 5.3 | Terborgh 1983 |
| <i>Saguinus mystax</i> | .576 | 40 | 1946 | 10 | 12 | Garber 1993a |
| <i>Saguinus labiatus</i> | .510 | 19.1 | 1487 | 7.5 | 16.67 | Buchanan-Smith 1991b |
| <i>Saguinus mystax</i> | .576 | 15.4 | 1991 | 9 | 2.8 | Peres 1992a and b |
| <i>Saguinus mystax</i> | .576 | 29 | 1248 | 9 | 14.9 | Norconk 1986 |
| <i>Saguinus mystax</i> | .576 | 31.5 | 2360 | 5.5 | 8.4 | Ramirez 1989 |
| <i>Saguinus oedipus</i> | .417 | 7.8 | 1700 | 9 | 40.1 | Neyman 1977 |
| <i>Leontopithecus caissara</i> | .572 | 321 | 2235 | 7 | 1 | Kierulff <i>et al.</i> 2002 |
| <i>Leontopithecus chrysomelas</i> | .578 | 36 | 1775 | 6.6 | 8.8 | Rylands 1982 |
| <i>Leontopithecus chrysomelas</i> | .578 | 40 | 1798 | 6.7 | 8.1 | Kierulff <i>et al.</i> 2002 |
| <i>Leontopithecus chrysomelas</i> | .578 | 93 | 1864 | 5 | 2.6 | Kierulff <i>et al.</i> 2002 |
| <i>Leontopithecus chrysopygus</i> | .575 | 138 | 1725 | 4.7 | 1.6 | Kierulff <i>et al.</i> 2002 |
| <i>Leontopithecus chrysopygus</i> | .575 | 277 | 1904 | 4.3 | .7 | Kierulff <i>et al.</i> 2002 |
| <i>Leontopithecus rosalia</i> | .609 | 45 | 1446 | 5.4 | 6.1 | Kierulff <i>et al.</i> 2002 |

^a Wild body masses are from sources listed in the table, or when not provided by the authors from Smith and Jungers (1997).

^b Group biomass calculations are based on the assumption that groups contain 2/3 adults (at full body mass) and 1/3 immatures (at 50% body mass). Thus biomass = [(body mass)(2/3 group size) + (body mass/2)(1/3 group size)] / (home range/100)

form long-lasting polyspecific associations (Buchanan-Smith 1999; Garber 2000; Heymann and Buchanan-Smith 2000; Norconk 1990; Peres 2000; Porter 2001a). If one assumes that food is limiting, then there should be high costs to tamarins and callimicos of forming polyspecific associations. However, previous studies of callitrichid polyspecific associations (Peres 1992a, b) showed no evidence of feeding competition. Instead, several authors have provided data indicating increased feeding advantages associated with increased troop size such as joint resource defense, increased effectiveness in locating feeding sites, and insect flushing (Garber 1988; Garber and Bicca-Marques 2002; Peres 1992b).

Although the day ranges of our subjects increased when polyspecific association rates increased, several observations suggest that it did not result from increased feeding competition. First, on 89.5% of observation days, there was no instance of contest competition between species (Porter and Garber 2007). When agonistic interactions occurred, the episodes were extremely brief, resulted in no injury, and accounted for <0.01% of the total activity budget (Porter and Garber 2007). Second, in a previous study of the benefits of polyspecific associations, Porter (2001a) found that during the wet season callimicos have higher feeding rates when in association with tamarins than when alone, and in the dry season when food availability might be expected to decrease, feeding rates did not change with association status. These patterns are opposite of what is expected under conditions of increased feeding competition. Many authors have proposed that individuals in polyspecific groups are able to lower their vigilance rates, allowing them more time to forage (Peres 1992a); however, callimicos in our study (Porter and Garber 2007) and a previous study (Porter 2001a) showed no decrease in vigilance during associations. Thus, the increase in feeding rates during associations does not appear to be the result of a decrease in vigilance behavior.

The correlation between longer day ranges and increased association rates likely results because callimicos exploit a wider variety of habitats, particularly more exposed areas, when associated with tamarins than when alone (Porter 2001a; Porter and Garber 2007). Callitrichids have many predators (Garber and Bicca-Marques 2002), and they respond to the predator calls of tamarins (Pook and Pook 1981; Rehg 2003). Thus, it is likely that callimicos enter a wider range of habitats when associated with tamarins because the mixed species group may reduce predation risk for its members by having more vigilant individuals across a wider range of forest strata than is possible when the callimicos are in a single-species, smaller, group (Porter 2001a; Porter and Garber 2007).

The size of the callimico group's home range is much larger than those of sympatric tamarin groups with which it associates at the site. For example, Suarez (2007) calculated a mean home range size of 23 ha for 3 groups of red-bellied tamarins at the site. As callimicos use the habitats of multiple tamarin groups, they regulate the frequency and duration of associations. Callimicos are generally first to initiate contact with a tamarin group, and they will also terminate associations to move into a different tamarin territory (Porter 2001a).

Hanson (2000) suggested that the larger home range size of callimico groups versus those of sympatric tamarin groups resulted from the callimicos tracking fungi resources across a wide area. Indeed, callimicos in this and earlier studies (Porter 2004; Rehg 2003) spent almost all of their time in the understory (0–5 m), where

fungi most likely occur (Porter 2004). Because the home range was larger in the dry season when mycophagy increased, there is some support for the hypothesis that home range size is influenced by the distribution and abundance of fungi. Porter (2001b) showed that mycophagy increased even as fungi availability declined, and that mycophagy occurs throughout the year. In contrast, fruit is a highly seasonal resource in northwestern Bolivia, and high rates of frugivory occur only during the wet season when fruits are most available (Porter 2001b). Hanson *et al.* (2006) performed nutritional analyses on the fungi eaten by callimicos, and found them to be low in nutritional value. The fungi contained complex structural carbohydrates and little protein. Fungi may represent a low-quality, fall-back food, eaten most frequently when higher quality fruits are scarce. Alternatively, callimicos, like marmosets, may have a specialized digestive system that allows them to break down the structural carbohydrates in fungi efficiently into volatile fatty acids and other nutrients. If so, fungi may be a good supplement to fruits as well as a reliable dry season food.

The only 2 other species of callitrichids that eat fungi frequently, *Callithrix aurita* (Correa 1995) and *Leontopithecus caissara* (Prado as cited in Raboy and Dietz 2004) also have very large home ranges as compared to other species within their genera (Table VI), providing additional support for the hypothesis that mycophagy requires large home ranges. Our results, however, show no correlation between monthly mycophagy and home range area, or day range for callimicos. The lack of a direct correlation between day range area, home range, and mycophagy, however, may be due to differences in the density and distribution of different types of fungi across the year.

Different fungi vary in their abundance and distribution, making them a highly variable resource. For example, Hanson (2000) found that in botanical plots (5 m×5 m) the dry mass of fungi consumed by callimicos ranged from 0 to 12.4 g (1–15 sporocarps) for bamboo fungi (*Asopolyporous*) and from 0 to 169.6 g (0–200 sporocarps) for jelly fungi (*Auricularia*). The fungi also occur on specific substrates (rotting logs and bamboo plants: Hanson 2000), and the substrates may be patchily distributed within the callimico group's home range. For example, our study group consumed 83% of fungi in secondary and bamboo forests, though the habitats accounted for only 21% of the home range area. Thus, the proximity of bamboo patches and decaying logs will influence the callimico foraging pattern. In addition, fungi can grow back where it was picked; thus fungal sites may remain sporadically productive over months or even years (Hanson 2000). Accordingly, fungal sites may serve as a reusable resource for callimicos, as tree exudates serve as a reusable resource for marmosets.

The data further suggest that as availability and abundance of bamboo and secondary forest habitats increase, home range size should decrease, allowing group densities to increase. At Rehg's study site, 44% of available habitat was bamboo and 3% secondary forest, and her callimico study group's home range was 59 ha, considerably smaller than in our study. In addition, Rehg noted that callimicos appear to prefer tree falls (Rehg *in press*), microhabitats that are likely to contain jelly fungi (Hanson 2000). Further, in surveys around the Pando, Porter (2006) found callimicos at high densities (5.7 groups/km²) only in an area with well established and extensive bamboo forest (Porter 2006). Thus, there is support for the contention that home range size is linked to the abundance of microhabitats containing fungi.

Similar relationships between food distribution, habitat availability, and ranging patterns are apparent in other callitrichids. For example, *Callithrix* and *Cebuella* are characterized by a foraging and ranging pattern in which a relatively small core area is reused over days or weeks. Because the genera have the ability to gouge holes in tree trunks to stimulate the flow of exudates (Rylands and de Faria 1993), they can create their own set of spatially concentrated (a single tree can have many exudate holes), productive, and renewable feeding sites (Soini 1993). Groups of *Cebuella* use the smallest home ranges of all Callithricidae (Table VI) and exploit exudate trees in a small core area for an extended time period of time from a few months to several years. Groups abandon the sites and move into new locals only when the principal exudate sources are depleted (Soini 1988).

In our study, the callimico group's use of its home range changed dramatically during the first 2 mo (Fig. 7b and c). Like *Cebuella*, *Callimico* may shift their core area over time, perhaps because resources have been depleted in one region of the forest. In addition to fungi, the abundance and distribution of other food resources such as exudates may influence callimico ranging patterns. For example, the callimico group that occupied a home range of 150 ha rarely consumed exudates (1% of annual diet, 1% of dry season diet; Porter 2001b), whereas our study group consumed exudates frequently in the dry season (14% of annual diet, 21% of dry season diet). Thus, the distribution and availability of not just 1 but several food types likely influences seasonal ranging patterns.

Tamarins and lion tamarins are characterized by larger day range and larger home ranges than marmosets (Table VI), which is likely to be a response to exploiting widely scattered and more ephemeral feeding sites, as well as increased patrolling of range boundaries. Mixed species groups of saddle-back and moustached tamarins that Peres (1992b) studied in Brazil and that Garber (1988, 1993a) studied in Perú had very different home ranges (150 ha vs. 40 ha), but similar day ranges (1991 m vs. 1850–1900 m). At both sites, the groups traveled across large areas of their range each day and commonly engaged in intergroup encounters at productive feeding sites and range boundaries (Garber 1988, 1993a,b; Peres 1992a). Thus, both the distribution of feeding sites and territorial interactions with neighboring groups play important roles in tamarin ranging behavior and patterns of habitat utilization.

Recent studies on lion tamarins indicate that groups may occupy home ranges of 36–321 ha, and day ranges of 1400–2235 m (Table VI), and their territorial behaviors also can vary considerably. Lion tamarin species at some sites have a ranging pattern similar to that of tamarins: groups search for resources distributed across a variety of microhabitats and travel to the borders of their ranges during territorial encounters (Kierulff et al. 2002). However, species at other sites show a different pattern in which groups occupy core areas within their range and less frequently engage in territorial behavior (Kierulff et al. 2002). For example, Kierulff et al. (2002) reported that golden lion tamarins at the Uniao Biological Reserve engage in intergroup encounters once every 16.7 d whereas at Poco Das Antas Biological Reserve, golden lion tamarins engage in intergroup encounters every 1.6–2.1 d.

Territorial encounters between callimico groups are rare. During our study, the callimico group encountered 1 extragroup male on only 2 d. A previous year-long study of callimicos at the same site showed similar results; intergroup encounters occurred on only 3% of all observation days. In contrast, intraspecific encounters

among *Saguinus fuscicollis* and *S. labiatus* neighboring groups were frequent (*S. fuscicollis*, 19% and *S. labiatus*, 38% of observation days: Porter, *unpub. data*). Rehg (2003) also observed infrequent intergroup encounters among callimico groups, which occurred on only 2 d of her 9-mo study. Thus, in contrast, to *Saguinus* and *Leontopithecus* (Peres 2000), patterns of range use and daily path length of callimicos are only minimally influenced by territorial behavior.

Finally, our data suggest that infant transport may influence ranging patterns. During September when the group's infant was 2 mo old, a time when the infant was transported >60% of the time (Porter 2001c), day ranges were 700 m, the smallest day range of any month. However, in October, the infant's third month, when infant transport occurs during *ca.* 40% of the time (Porter 2001c), the day range was 870 m, larger than the ranges reported for 5 other mo. Additional data on ranging patterns and infant transport are necessary to determine how the costs of transporting single infants in callimico groups influence ranging behavior as compared to other callitrichids.

Our data suggest callimicos have a ranging and foraging pattern unlike any other callitrichid. Callimico groups are characterized by relatively large home ranges (similar to *Saguinus* and *Leontopithecus* in some areas), but relatively short day ranges. We propose that callimico ranging patterns are influenced by 3 related factors: 1) a foraging pattern characterized by the exploitation of resources (fungi) and microhabitats (bamboo forests and wet secondary forests) that are highly scattered; 2) the absence of territorial defense; and 3) shifting of core areas when sources of fungi are no longer productive. Because all studies of callimicos to date have been of single groups, the degree of range overlap or unoccupied space that exists between groups remains to be determined. The additional data are necessary for conservation planning in order to accurately estimate the density of callimicos across their geographic range.

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