Vertical clinging and leaping in a neotropical anthropoid

Napier and Walker' proposed a new category of primate locomotor behaviour which they called "vertical clinging and leaping". They believed that among living primates this category included only certain prosimians. It has since been recognised that non-prosimian primates (for example, Saquinus2, Cacajao3, and Callicebus4) may at times also leap to and from postures in which the body is held vertically at rest. In a recent review of vertical clinging and leaping Stern and Oxnard suggest that "future behavioural observations will show that almost all primates may occasionally move in this way". In view of the acrobatic arboreal abilities of primates this would not seem remarkable, given appropriate environmental conditions and stimuli. So far, however, no one has reported any anthropoid primate engaging habitually in this form of positional' behaviour.

From July to September, 1974, we observed a group of nine pygmy marmosets, Cebuella pygmaea, for over 200 h in inundatable forest at the edge of the Nanay river, about 30 km south-west of Iquitos, Peru. The group consisted of four adults, three subadults, and two infants carried by an adult male. (A comprehensive study of this group, including a detailed presentation of methods, is being prepared by M. Ramirez.) The vegetation was virgin tropical rain forest with a continuous canopy between roughly 10 and 20 m high, and a few emergent trees up to 35 m. Relatively heavy undergrowth existed below the canopy, including many bushes and lianas of varying size. The marmosets were normally awake for about 11.5 h each day, from 0615 to 1745. By quantifying frequency and duration of activity patterns for 4d, we found that adult animals spend approximately 48%, of their time feeding (including foraging for insects), 12% moving (exclusive of locomotion involved in feeding), and 40% resting (including grooming). We obtained the following data on adult animals while noting whether the substrate was more or less horizontal (less than 45° inclination) or vertical (greater than 45°). During 16 h observation of feeding behaviour, 77%, of the animals' time was spent clinging to vertical supports of large diameter while feeding on sap. Cebuella used a wide range of locomotor behaviours, including quadrupedal walking and running along supports as well as leaping between supports. We observed leaps of up to 2 m which confirms the observations of Christen on captive Cebuella6. We observed and counted 288 leaps over several days and of these 38% were from one vertical support to another, 28% from a horizontal to a vertical, 19% from a vertical to a horizontal, and only 15% were from a horizontal to a horizontal. Thus, a total of 85% of all leaps observed were to and/or from a vertical supporting branch. Animals spent 57% of their resting time (48 h observation) clinging to vertical supports. The longest period during which an adult individual clung continuously to a vertical support without moving was 96 min; the longest period that an animal was observed sitting on a horizontal support was 16 min. We believe these data amply justify consideration of Cebuella pygmaea as a neotropical vertical clinger and leaper.

Cebuella is a tiny animal, the smallest New World monkey and the second smallest primate; average weight of adults is 145 g (ref. 7). It spends most of its feeding time obtaining and eating sap, a behaviour which has also been noted for Cebuella in Columbia by Moynihan. In addition Cebuella feeds on insects and berries. Insects and spiders are approached by slow stalking and are frequently captured using a rapid pouncing leap. Most insect foraging occurs in areas of entangled lianas and bushes below the level of the closed canopy (the primary foraging zone). This substrate,

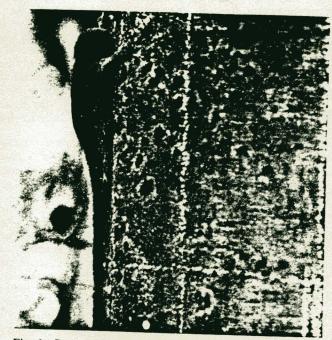


Fig. 1 Posture of adult Cehuella while feeding on sap of Quararibea sp. (Bombacaceae).

in contrast to the canopy, has a relatively high frequency of vertical supports. An individual may spend 85 to 90 of its total waking hours in the primary foraging zone. Berries ('renaco', Ficus sp., and 'caymittillo') are an infrequent source of food, and are procured from terminal branches in the canopy (that is, a secondary foraging zone), or from bushes below it.

In terms of time spent, sap was the most important food resource for Cebuella during our study. Sap was obtained from lianas and from the trunks of trees of both large and small diameter. Cebuella obtained this exudate by using its semiprocumbent lower incisor teeth to scrape fissures into the bark, primarily while clinging to large vertical tree trunks. The trunk diameter of the preferred sap-feeding tree (Quararibea sp., Bombacaceae) measured 51 cm at the feeding level. Adult individuals spent an average of 97 min each day preparing, and/or feeding at, sap-holes on this large tree alone. The sap of other large diameter trees, including Palicourea macrobotrys (Rubiaceae), was also used for feeding. Throughout these feeding bouts on large tree trunks a variety of clinging postures were used, with the body oriented upright, inclined, or head downward. In the latter posture the lower extremity was rotated laterally. In the upright position the base of the tail was often pressed to the tree trunk; the forelimbs were either abducted and fully extended (Fig. 1) or adducted at the shoulder and partially flexed at the elbow; the hindlimbs were widely abducted indicating great hip mobility, or closely adducted and flexed beneath the body. In all these postures the claws of Cebuella served a particularly important function specific to feeding. During scraping actions of the teeth against the bark, the manual claws anchored the forelimbs laterally, while the pedal claws anchored the hind limbs below (Fig. 1). The head (and often the shoulders) was fixed on the vertebral column. The forelimbs acted as levers, flexing at the elbow and/or wrist, increasing the mechanical advantage at the mandibular incisors. Most important, during all postural behaviours on large substrates the claws seemed to be firmly embedded in the bark.

Napier and Walker¹, in recognising vertical clinging and leaping as a distinct locomotor category, suggested a fairly precise correlation between its behavioural and morpho-

logical features. Stern and Oxnard³ pointed out, however, that multivariate analyses of the various components of the locomotor skeleton "suggest that there is more than one kind of morphology among vertical clingers and leapers and, therefore, that there is likely to be more than one kind of vertical clinging and leaping." They distinguished two such kinds, one for the indriids, and a second for Microcebus, Galago, and Tarsius; subsequently Oxnard10 suggested a third mode manifested by Lepilemur. Jouffroy and Gasc11 distinguished the same three locomotor groups based on morphology presumed to be adapted specifically for leaping and not for clinging.

Our data indicate that claws in Cebuella are for clinging to large vertical supports, and are not part of a complex related to leaping. We do not yet know what is the adaptive relationship between leaping and vertical clinging; Cebuella

does both.

In Cebuella vertical clinging involves grasping (of slender supports) with the hallux, but also involves clinging to broad supports with the claws of both hands and feet. As Cartmill has pointed out, clawed primates are generally more competent than clawless ones of similar body size in moving on thick vertical supports. Vertical positional behaviour offers the pygmy marmosets their only (or at least their most efficient) access to sap, an apparently essential food resource. Clinging is a postural not a locomotor adaptation. Failure to distinguish between posture and locomotion may overlook the biological importance of clinging which in Cebuella is clearly related to feeding. Differing biological functions for vertical clinging have probably evolved in different primate lineages. Clinging and leaping faculties may or may not be part of the same form-function complex12, the observed differences in morphology arising from this.

We conclude that in Cebuella, semiprocumbent mandibular incisors, small body size and clawed digits are part of an adaptive complex especially related to feeding on sap while clinging to large vertical supports. Similarly, Galago elegantulus13, Phaner furcifer and Microcebus coquereli14, of medium body size, with very procumbent mandibular incisors, and modified nails which function as claws, also feed on sap while clinging to large tree trunks¹⁵. Thus, there is an evolutionary convergence in biological role (not

in diagnostic vertical clinging and leaping morphology) of vertical clinging adaptations to exploit sap-feeding niches in certain medium-sized nocturnal galagines and cheirogaleines, and in the small diurnal Cebuella pygmaea.

This suggests that vertical clinging behaviours are postural adaptations, related to feeding and dependent on the size of the support and on the spatial location of the food resource. Leaping behaviours, on the other hand, are locomotor adaptations. Thus, they serve different biological functions which may or may not be related to obtaining food.

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