Locomotion of New World monkeys: Interactions of intrinsic and extrinsic factors

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Abstract

The diversity of locomotor modes encountered in primates suggests a continuous interaction of intrinsic factors related to morphology (e.g., body weight, diet, locomotor modes) with extrinsic ones related to habitat structure (e.g., forest architecture, spatio-temporal distribution of resources, structural properties of available branches). This diversity offers solutions to problems imposed by the surrounding milieu and largely contributes to the evolution of adaptive niches in primates, and most particularly in New World platyrrhines. This report treats first-hand locomotion-associated data collected by first encounter and 20-sec instantaneous sampling in two forests in French Guiana and Ecuador. The matrix of recorded factors, including body weight, concerning thirteen different platyrrhine species was subjected to cluster analyses in order to assess the interaction between some intrinsic and extrinsic factors in platyrrhines. When the different species were treated as variables, atelines and pitheciines were clustered together supporting the atelid clade. Cebuella was always at the base of every cluster diagram, while Callicebus was always associated with the Cebinae and Callitrichinae. When the different factors were used as variables, all cluster diagrams produced two more or less consistent clusters. Mature forest, canopy use, and frugivory clustered together. This group of factors appears to best illustrate the adaptive niche of the Atelinae.

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On the other hand, animalivory, leaping, and understorey use were also grouped together, usually accompanied by a cluster formed by liana forest use, liana use, and the use of vertical supports. This array of factors seems to best describe the adaptive radiation of the Callitrichinae. The cluster analyses suggest complex relations between the different locomotor-associated intrinsic and extrinsic parameters that determine the major adaptive radiations in platyrrhines.

**Mots clés**: platyrrhiniens, analyse en "clusters", locomotion, régime alimentaire, habitat.

**Key words**: platyrrhines, cluster analysis, locomotion, diet, habitat structure.

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**INTRODUCTION**

Locomotion, active body displacement within the environment, and posture, active maintenance of immobility, allow primates, as well as other animals to exploit food sources, to escape from predators, as well as to approximate mates in order to enhance reproductive success and survival (Terborg, 1983; Cant, 1992). In primates that are largely confined to subtropical and tropical forest canopies, locomotor and postural patterns display a great diversity. These diverse locomotor and postural modes, known as the positional behaviour (Prost, 1965), are the result of constant interactions between intrinsic factors, related to morphology, and extrinsic ones, related to habitat architecture. Intrinsic factors, such as body weight, diet, body dimensions, proportional and osteo-muscular morphology determine local functions that sum up to movements that are coordinated to certain modes. In their turn, these modes appear as solutions to problems emerging by extrinsic factors, such as climate, food or predator spatio-temporal availability and location, tree crown architecture, as well as mechanical and structural properties of available arboreal supports. The components of this continuous interaction are well associated with the great variety of locomotor and postural modes in primates, a fact further reflected in the diversity of their postcranial morphology (Cant, 1992).

However, although the evolutionary importance of positional behaviour has been repeatedly underlined (Washburn, 1951; Napier 1967; Ripley 1967), the body of the concerned literature is relatively small, in comparison to ecological and behavioural studies. Fortunately, an increasing number of detailed quantitative studies accumulate ever since the first study
by Ripley (1967). The majority of these studies of primate positional
behavior focus on New World primates, the platyrhines (see Dagosto &
Gebo, 1998) since they exhibit a great diversity in size, as well as dietary
and locomotor/postural adaptations (Rosenberger, 1992).

In effect, the body size of platyrhines ranges from the 116 g of the
smallest anthropoid, Cebuella pygmaea, to the 9,610 g of Brachyteles
arachnoides (Smith & Jungers, 1997), and by contrast to most catarrhines,
they are mainly, if not exclusively, arboreal. The smallest representatives,
the Callitrichinae, possess claw-like tegulae and exploit the lower layers
of the forest where they can claw-climb and leap between vertical trunks
and twigs in search of gums (Cebuella, Callithrix) and invertebrate prey
(Saginus) that represent the major part of their diets (Garber, 1992; Rylands,
1996). Callicebus, a member of the Pitheciinae (Rosenberger, 1981) or the
Aotinae clade of the Cebidae (Ford, 1986), is a quadruped and leaper, that
exploits the lower forest layers confined to a frugivorous-folivorous diet
(Kinzey, 1992). Its close relative, Aotus, the only nocturnal anthropoid,
moves by walking and leaping within the canopy feeding mainly on fruit
and insects (Wright, 1992). The medium-sized Cebinae, Cebus and Saimiri,
appear to exploit all forest layers, where they move by quadrupedal walk
and leaping, exploiting various vegetal and animal food sources through
their developed manipulative dexterity (Janson & Boinski, 1992). The
medium to large sized Atelidae involve two clades: The Pitheciinae sensu
Ford (1986), Pithecia, Cacajao, and Chiropotes, walk and leap in the
canopy where they prey on immature fruit and seeds (Kinzey, 1992). The
larger Atelinae, Alouatta, Ateles, Lagothrix, and Brachyteles, present high
rates of folivory (Alouatta, Brachyteles), frugivory-animalivory (Lago-
thrrix), and specialised frugivory (Ateles) and exploit the higher forest layers
where they frequently climb and suspend (Rosenberger & Strier, 1989).
This adaptive diversity of platyrhines suggests a constant interaction
between several morphological (intrinsic) features and the spatio-temporal
architecture and phenology of neotropical forests (Ford, 1986, 1988; Ford
& Davis, 1992; Rosenberger, 1992). Among morphology-related features,
locomotor and dietary adaptations appear to play a prominent role in the
evolution of adaptive niches (Rosenberger, 1992).

Under this perspective, the goal of this report is to examine the inter-
relations between these intrinsic and extrinsic factors. For this purpose I
used several locomotion-related parameters collected in two distant neo-
tropical forests. These parameters were divided into morphology-related
parameters (intrinsic) and habitat-related parameters (extrinsic). The intrin-
sic parameters examined represent each species: body weight, locomotor
mode, and diet. Body weight is a life parameter of extreme importance and was included in the analysis using data from the literature (Smith & Jungers, 1997). Locomotor mode is mainly determined by the osteo-muscular anatomy of the axial and appendicular systems, while diet is directly linked to body mass, dentition, as well as the anatomy of both masticatory and digestive systems. The diversity of locomotor modes and diets compose the intrinsic factors that would characterise a certain species. On the other hand, the extrinsic parameters examined describe the environment wherein the subject species live: Forest type and layer, support type, size, and orientation. The various forest types and layers, and different support types, sizes and orientations illustrate the extrinsic factors that determine the physical features of the environment and interact constantly with the intrinsic features. Thus, each species would be represented by a multidimensional array of intrinsic and extrinsic factors and the use of every factor could be associated with one or several species. Therefore, I used cluster analyses that could reveal clusters of species or factors in order to (a) compare the adaptive zones of sympatric species in two distant forests, and (b) elucidate the interactions between intrinsic and extrinsic factors as revealed through the studied primate communities.

FIELD STUDIES

The data for this analysis originate from two field studies: one in central French Guiana in the north-eastern part of South America and one in Ecuadorian Amazonia, in the north-western part of the Amazon basin. Both study sites are located in the opposite extremities of an east-west Amazonian gradient, belonging to different Pleistocene refugia. Both forests are mainly terra-firme high mature rain forests that involve primate communities of six (French Guiana) and ten (Ecuador) platyrrhine species. Since two species were rarely encountered and one (red howlers) is found in both forests I obtained data for 13 different species. However, it would have been easier to collect similar data from the literature in order to obtain a larger sample of study sites, enhancing the number of species and forest types and approximating the platyrrhine adaptive diversity. This would not have been advisable since the available data would come from different sources that have employed different methods in data acquisition and definition. Being aware of this problem arising from the inadequacy of data comparability in studies of primate positional behaviour (Dagosto & Gebo,
1998), I decided to analyse personal data, where the same data acquisition methods and definition of variables have been used.

The field study in French Guiana was conducted in the "Station des Nouragues" site (04°05´N, 52°40´W) within the Nouragues Reserve. The research station is run by the Centre National de la Recherche Scientifique and the Museum National d'Histoire Naturelle. The site is dominated by terra firme high mature rain forest with smaller patches of other forest types, and is described in detail elsewhere (Juilliot & Sabatier, 1993). The data were collected between April-July 1992 (wet season), and between July-September 1993 (transitional and early dry season). The data concern the five of the six species of the primate community: red howlers (*Alouatta seniculus*), black spider monkeys (*Ateles paniscus*), brown capuchins (*Cebus apella*), wedge-capped capuchins (*Cebus olivaceus*), and golden-handed tamarins (*Saguinus midas*); I did not obtain any data for the shy and rarely encountered sakis (*Pithecia pithecia*).

The field study in Ecuador was conducted in the "Proyecto Primates" site (00°42´S, 76°28´W) located in km 47 of the Pompeya Sur-Iro road of Maxus Ecuador Inc. within the Parque Nacional Yasuni, Napo Province. The research station is run by the University of California at Davis, New York University, and the Pontificia Universidad Catolica del Ecuador. The site is dominated by terra firme high mature rain forest with smaller patches of other forest types and is described elsewhere (DiFiore & Rodman, 2001). The data were collected between April 1995 and September 1996 covering all seasons. The data concern the nine of the ten species of the primate community: common woolly monkeys (*Lagothrix lagothricha*), red howlers (*Alouatta seniculus*), white-bellied spider monkeys (*Ateles paniscus*), monk sakis (*Pithecia monachus*), duski titi (*Callithecus cupreus*), white-fronted capuchins (*Cebus albifrons*), common squirrel monkeys (*Saimiri sciureus*), golden-mantle tamarins (*Saguinus tripartitus*), and pygmy marmosets (*Cebuella pygmaea*); I did not obtain any data for the nocturnal owl monkeys (*Aotus vociferans*).

**METHODS OF DATA ACQUISITION AND ANALYSIS**

In both sites I collected two sets of locomotion-associated data (Table 1): One set of data was collected through first sight. In this case, I recorded several parameters (Table 1) right after the first encounter with the primates (see also Mittermeier & Roosmalen, 1981). The other set comprised data recorded at 20-sec intervals. In this case, I used the focal animal instan-
taneous sampling method (Altmann, 1974) where I discreetly followed a focal primate recording several parameters (Table 1) every 20 seconds determined by a stopwatch. Both sets of data are presented in the form of tables. For the first sight data, each row corresponds to an independent encounter and each column to a recorded parameter. Similarly, for the focal instantaneous data each row corresponds to an instant and each column to a recorded parameter. For both data sets, the percentages of use for every parameter for each species were calculated. Parts of the data presented here

Table 1
Recorded parameters (first column) with the examined factors (second column) in the field studies in French Guiana and Ecuador used in the cluster analysis [(1) extrinsic parameter, (2) intrinsic parameter]

<table>
<thead>
<tr>
<th>First sight (first encounter)</th>
<th>Code</th>
</tr>
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<tr>
<td>Forest type (1)</td>
<td></td>
</tr>
<tr>
<td>Mature forest</td>
<td>MATFOR</td>
</tr>
<tr>
<td>Liana forest</td>
<td>LIAFOR</td>
</tr>
<tr>
<td>Forest layer (1)</td>
<td></td>
</tr>
<tr>
<td>Canopy</td>
<td>CANOPY</td>
</tr>
<tr>
<td>Understorey</td>
<td>UNDER</td>
</tr>
<tr>
<td>Diet (2)</td>
<td></td>
</tr>
<tr>
<td>Fruit</td>
<td>FRUIT</td>
</tr>
<tr>
<td>Leaves (flush and mature)</td>
<td>LEAVES</td>
</tr>
<tr>
<td>Animal matter (invertebrates/vertebrates)</td>
<td>ANIMAL</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Focal animal instantaneous sampling</th>
<th>Code</th>
</tr>
</thead>
<tbody>
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<td>Support type (1)</td>
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<td>LIANA</td>
</tr>
<tr>
<td>Support size (1)</td>
<td></td>
</tr>
<tr>
<td>Small (≤ 2 cm)</td>
<td>SMALL</td>
</tr>
<tr>
<td>Large (≥ 10 cm, ≤ 20 cm)</td>
<td>LARGE</td>
</tr>
<tr>
<td>Support orientation (1)</td>
<td></td>
</tr>
<tr>
<td>Horizontal</td>
<td>HORIZ</td>
</tr>
<tr>
<td>Vertical</td>
<td>VERTIC</td>
</tr>
<tr>
<td>Locomotor mode (2)</td>
<td></td>
</tr>
<tr>
<td>Arboreal quadrupedal walk</td>
<td>QUAD</td>
</tr>
<tr>
<td>Climb/suspension</td>
<td>SUSP</td>
</tr>
<tr>
<td>Leap (vertical and between twigs)</td>
<td>LEAP</td>
</tr>
</tbody>
</table>

Tableau 1
Paramètres enregistrés (1re colonne) et ses facteurs examinés (2me colonne) durant les études de terrain en Guyane et en Equateur utilisées dans les analyses des cluster [(1) paramètre extrinsèque, (2) paramètre intrinsèque]
have been published elsewhere (Youlatos, 1999; Youlatos & Gasc, 2001; Cant, Youlatos, & Rose, 2001).

For every recorded parameter the calculation of percentages revealed the most important states that could characterise the species studied. Therefore, although for every kind of recorded parameter I obtained percents for the different recorded factors (e.g., for forest type: Mature forest, Liana forest, Low forest, Secondary forest and others), for the purpose of this study I shall only treat those shown in the second column of Table 1 (e.g., for Forest type I kept the percentages of Mature forest and Liana forest use). To these factors I added body weight from the literature (Smith & Jungers, 1997), since it is a life parameter of paramount importance in animal biology. But since the platyrrhines examined present almost a 100-fold differences in magnitude of body weight (Cebuella vs. Ateles; Tables 2, 3), I used the normal deviate (Z) to standardise the body weight values. Z indicates the number of standard deviations from the mean for every value and standardises or normalises the values (in this case body weights that are encoded as STDZBW) for the analyses (Zar, 1996). After having selected the percentages of variables and having standardised body weights, each of the 13 studied species would be represented by 16 different quantitative variables.

Therefore, since the purpose of this report is to treat the interrelations between the intrinsic and the extrinsic factors shown in Table 1, the calculated percentages of use of each factor for each species plus standardised body weight were used in cluster analyses. Clustering methods would help diagnose groups of either species or factors that are well associated and would form strongly interacting units that would eventually illustrate the adaptive zones of platyrrhines. The percentages of use of factors and the standardised body weight formed the new matrix of input data. In order to calculate distances between the clustered variables (factors or species), I used euclidean distances that measure geometric distances in space. In this case, two factors or species are identical when they are described by variables with the same magnitude and their distance is zero (Aldenderfer & Blashfield, 1984). Therefore higher distances represent distant bonds and lower ones closely related groups. Among hierarchical agglomerative methods, I used Ward’s method that is designed to optimise the minimum variance within clusters. It is considered as the most efficient method since it uses an ANOVA approach to evaluate the distances between clusters and tends to create clusters of relatively equal sizes (Aldenderfer & Blashfield, 1984). I performed two different cluster analyses for each site (French Guiana, Ecuador) and two different ones using the combination of data from
both sites, resulting to a total of six cluster diagrams. In the first set of clusters I used species as the clustered variables (Figures 1, 3, 5). In these diagrams, each species is described by its attributed factors and I could assess relationships between different sympatric species, as well as adaptive relationships between different groups of species. In the other set of clusters, I used factors as the clustered variables (Figures 2, 4, 6). In these diagrams, I could assess the interaction of different factors contributing to specific adaptive niches that can be associated with the biology of platyrhine species or subfamilies.

Table 2
Percentages of factor use by the primate community of French Guiana (* Smith and Jungers, 1997)

<table>
<thead>
<tr>
<th></th>
<th>Alouatta seniculus</th>
<th>Ateles paniscus</th>
<th>Cebus apella</th>
<th>Cebus olivaceus</th>
<th>Saguinus midas</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body weight (g)</td>
<td>5,950</td>
<td>8,775</td>
<td>3,085</td>
<td>2,905</td>
<td>545</td>
</tr>
<tr>
<td>Mature forest</td>
<td>78</td>
<td>97</td>
<td>44</td>
<td>82</td>
<td>51</td>
</tr>
<tr>
<td>Liana forest</td>
<td>1</td>
<td>0</td>
<td>27</td>
<td>12</td>
<td>9</td>
</tr>
<tr>
<td>Understorey</td>
<td>1</td>
<td>0</td>
<td>28</td>
<td>25</td>
<td>73</td>
</tr>
<tr>
<td>Canopy</td>
<td>97</td>
<td>98</td>
<td>72</td>
<td>75</td>
<td>27</td>
</tr>
<tr>
<td>Lianas</td>
<td>11</td>
<td>6</td>
<td>8</td>
<td>10</td>
<td>14</td>
</tr>
<tr>
<td>Horizontal</td>
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</tr>
<tr>
<td>Vertical</td>
<td>6</td>
<td>2</td>
<td>6</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>Small</td>
<td>40</td>
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<td>20</td>
<td>18</td>
<td>6</td>
<td>10</td>
<td>21</td>
</tr>
<tr>
<td>Quadrupedal walk</td>
<td>37</td>
<td>20</td>
<td>32</td>
<td>32</td>
<td>32</td>
</tr>
<tr>
<td>Climb-suspend</td>
<td>54</td>
<td>74</td>
<td>39</td>
<td>38</td>
<td>28</td>
</tr>
<tr>
<td>Leap</td>
<td>3</td>
<td>3</td>
<td>24</td>
<td>27</td>
<td>26</td>
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<td>Fruit</td>
<td>69</td>
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<td>54</td>
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<td>1</td>
<td>6</td>
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<tr>
<td>Animal matter</td>
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<td>0</td>
<td>47</td>
<td>33</td>
<td>31</td>
</tr>
</tbody>
</table>

Tableau 2
Pourcentages d'utilisation de différents facteurs de la communauté des primates en Guyane Française (* Smith et Jungers, 1997)
<table>
<thead>
<tr>
<th>Factor</th>
<th>Alouatta seniculus</th>
<th>Ateles belzebuth</th>
<th>Lagothrix lagothricha</th>
<th>Cebus albifrons</th>
<th>Pithecia monachus</th>
<th>Saimiri sciureus</th>
<th>Callicebus cupreus</th>
<th>Saguinus tripartitus</th>
<th>Cebuella pygmaea</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body weight (g) *</td>
<td>5,950</td>
<td>8,070</td>
<td>7,150</td>
<td>2,735</td>
<td>2,360</td>
<td>720.5</td>
<td>1,070</td>
<td>350.5</td>
<td>116</td>
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<td>89</td>
<td>74</td>
<td>74</td>
<td>35</td>
<td>52</td>
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<tr>
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<td>1</td>
<td>11</td>
<td>0</td>
<td>15</td>
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<td>1</td>
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<tr>
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<td>9</td>
<td>47</td>
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<td>62</td>
<td>75</td>
<td>89</td>
</tr>
<tr>
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<td>83</td>
<td>88</td>
<td>51</td>
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<tr>
<td>Quadrupedal Walk</td>
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<td>Climb-Suspend</td>
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<td>61</td>
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<td>74</td>
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</table>
RESULTS

Primate community of Nouragues in French Guiana

The clustered platyrrhine species of French Guiana seem to follow their phylogenetic relationships (5 species, Figure 1). The Atelinae (Alouatta, Ateles) are clustered apart from the rest of the community displaying a strong relationship (distance: 45.34), less stronger than the group of the two syntopic capuchins (C. apella - C. olivaceus distance: 44.28).

Figure 1. Cluster diagram of the 5 species of the Nouragues primate community in French Guiana.

Figure 1. Diagramme en clusters des 5 espèces de la communauté des primates de Nouragues en Guyane française.
On the other hand, the clustered factors presented some noticeable groupings (Figure 2). A cluster including mature forest use, frugivory and canopy use, is set apart from the one containing liana forest use and leap, grouped along with animalivory. Other distinct clusters grouped quadrupedal walk with horizontal support use, and climb/suspend with use of small supports.

Figure 2. Cluster diagram of the 16 extrinsic and intrinsic factors of the Nouragues primate community in French Guiana.

Primate community of Yasuni in Ecuador

The platyrrhine species of Yasuni are clustered in groups that reflect some of their phylogenetic relationships (9 species, Figure 3). Lagothrix and Ateles are strongly related (distance: 39.06), and group together with Pithecia instead of their closer relative, Alouatta. However, all together appear to support the Atelid clade. The Cebinae (Cebus, Saimiri) also form a solid group (distance: 46.94). The callitrichine Cebuella is divergent from all other platyrrhines, and more particularly, the other callitrichine Saguinus, that is grouped with Callicebus, and the Cebinae.

Figure 3. Cluster diagram of the 9 species of the Yasuni primate community in Ecuador.

The cluster diagram representing clustered factors from Yasuni appears to have preserved some of the grouping of the cluster diagram from French Guiana (Figure 4). Thus, animalivory is grouped along with leap and the use of understorey. Another cluster is created by canopy use and mature forest use. Quadrupedal walk is once more related to use of horizontal supports, while a new cluster contains climb/suspend with folivory and body weight.

Figure 4. Cluster diagram of the 16 extrinsic and intrinsic factors of the Yasuni primate community in Ecuador.

Combined primate communities

The use of all studied species produced cluster diagrams with rather confused groups (14 species, Figure 5). A first diagnose is the two separate groups involving the Atelinae-Pitheciinae versus the rest of the platyrrhines. Moreover, *Cebuella* persists in its very divergent position. Sharing the same forest appears to play a major role, since sympatric species tended to group together: *Alouatta-Ateles paniscus* and *Cebus apella-Cebus olivaceus* in French Guiana, or *Alouatta-Pithecia* and *Saimiri-Cebus albifrons* in Yasuni instead of grouping with their respective congeners. The Callitrichinae did not present any coherence.

Figure 5. Cluster diagram of the 14 species of both primate communities.

**Figure 5. Diagramme en clusters des 14 espèces appartenant aux deux communautés de primates mises ensemble.**

(Pour le calcul des distances, voir méthodes.)
By contrast, clustered factors seem to support clusters presented in former cluster diagrams (Figure 6). Hence, mature forest use and canopy use are grouped together. Quadrupedal walk is once more linked to the use of horizontal and large supports, while frugivory, climb/suspend and use of small supports are grouped together. On the other hand, animalivory, leap and understorey use are once more clustered together. Lastly, a distinct cluster groups liana forest use, lianas, and vertical support use.

**Figure 6. Cluster diagram of 16 extrinsic and intrinsic factors of both primate communities.**

DISCUSSION

Platyrrhine species associations

Most clusters produced with the platyrrhine species as variables appear to have respected the major phylogenetic relationships among the group (Rosenberger, 1981; Ford, 1986). The Atelinae (Alouatta, Ateles paniscus, A. belzebuth, Lagothrix), comprising the large prehensile-tailed monkeys, seem to persist as a group different from the other platyrrhines (but see Figure 5). In effect, their large size, appendicular morphology, truly prehensile tails that enable climbing and suspensory habits, and their tendency to a herbivorous diet (although Lagothrix spends a considerable amount of time foraging for animal prey; DiFiore and Rodman, 2001) reflect a quite specialised group that justifies its divergence from the other platyrrhines (Rosenberger, 1981; Ford, 1986; Rosenberger & Strier, 1989; Strier 1992).

The Pitheciinae sensu Ford (1986), represented here by Pithecia, were always clustered with the Atelinae, supporting the Atelidae family. On the other hand, the Pitheciinae sensu Rosenberger (1981), comprising both Pithecia and Callicebus in the study sites, were not supported by my findings. Rosenberger (1981, 1992) identified in Callicebus a model for the primitive pitheciine, but its position in the diagrams associated with the Cebinae and Callitrichinae seems to support adaptations similar to most small or medium-sized platyrrhines. This may lend support to Ford’s considerations of Callicebus as the model for the primitive platyrrhine (Ford, 1986, 1988; Ford & Davis, 1992). However, recent discoveries and descriptions of the most primitive platyrrhine, Bransicella boliviana, have presented some dental features (e.g., high crowned molars) that imply different dietary and positional adaptations from that inferred by the biology of Callicebus (Takai & Anaya, 1996; Takai, Anaya, Shigehara, & Setoguchi, 2000).

As far as the Callitrichinae are concerned (Saguinus midas, S. tripartitus, Cebuella), the results show they were in no way clustered together (Figures 3, 5). This may be related to the fact, that although they bear several gross adaptive similarities as a group, they do present a significant variety in their dietary and positional adaptations (Garber, 1992). More precisely, the very divergent position of Cebuella in respect with the other platyrrhines is noteworthy. The diminutive size of Cebuella, accompanied by dietary (obligate gumivory) and habitat use particularities (small territories, patchy distribution, few exploited feeding trees, frequent vertical leaping and claw climbing, territorial and aggressive behaviour) contribute
Locomotor behaviour in platyrrhines to a quite distinct adaptive form, divergent from the rest of platyrrhines (Soini, 1988; Garber, 1992; Ferrari, 1993; Harrison & Tardiff, 1994; Rylands, 1996; Youlatos 1999). On the other hand, the different *Saguinus* species-groups exhibit different positional patterns and dietary preferences (Garber, 1991, 1992). *S. midas* feeds mainly on small fruit and insects located in tree crown extremities where it walks and leaps and is only seasonally based on tree exudates and trunk foraging, similar to *S. mystax* and *S. geoffroyi* (Mittermeier & van Roosmalen, 1981; Garber, 1992). By contrast, *S. tripartitus* appears to use more vertical trunk ranging and leaping in search of fruit, insects, and nectar, most likely similar to its close relative *S. fuscicollis* (Garber, 1992; Kostrub, 1997; Youlatos, 1999).

Another interesting issue arising from the results is the influence of sympatry, which appeared to be in some cases stronger than that of phylogenetic relationships. Hence, in the combined data analysis, the Yasuni Atelinae formed a separate cluster from the Nouragues Atelinae, whereas sympatric Pithecia and Alouatta in Yasuni were more closely related to each other than Alouatta was with the other Atelinae (Figure 5). The same occurred within the Cebinae, where Cebus albipons and its sympatric Saimiri in Yasuni were clustered together, rather than with its congeners from Nouragues. These results may not come to any surprise if one considers that the data used for each species describe its way of exploiting forest architecture through its own morphology. Therefore, species dwelling in the same forest and dealing with related problems would appear to be closer together than with a close relative that would interact differently with another forest's architecture. Thus, sympatric platyrrhines would have more in common than close relatives, especially if one considers that platyrrhine phylogenetic groups actually represent adaptive radiations to specific niches (Rosenberger, 1992).

On the other hand, the fact that red howlers, *Alouatta seniculus*, which occur in both sites, were clustered in different groups seems interesting (Figure 5). In the diagrams describing French Guiana (Figure 1) and combined data (Figure 5), *A. seniculus* of Nouragues (ALOUN) is clustered with the spider monkeys (*Ateles paniscus*). On the other hand, the red howlers of Yasuni (ALOUY) are clustered closer to Pithecia in the diagrams describing Ecuador (Figure 3) and combined data (Figure 5). In French Guiana, howlers exploit the higher forest layers, are highly frugivorous, climb considerably and use high rates of small supports (Juillot & Sabatier, 1993; Youlatos & Gasc, 2001), whereas in Ecuador, howlers consumed more leaves, were principally quadrupedal walkers and used higher rates of large, horizontal supports. These differences may reflect the
adaptive plasticity of howlers. The different demands imposed by the structure of different forests, as well as potential competition for food sources by other representatives of the primate community, compel howlers to adopt different strategies in different forests. Howling monkeys are indeed among the most easily adaptable monkeys since they can be found in forest fragments, secondary and degraded forests showing a large geographical distribution covering many different forested and edge habitats (Rosenberger & Strier, 1989; Strier, 1992).

**Interrelations between intrinsic and extrinsic factors**

Cluster diagrams that used factors as the clustered variables revealed groups of factors that apparently interact together and form units that would characterise adaptive niches among the primate species studied. Thus, among these diagrams consistent patterns of clusters seemed to emerge. Mature forest use grouped along with canopy use, as well as with frugivory either directly (Figure 2; Nouragues) or indirectly (Figures 4, 6; Yasuni and combined). Frugivory was also related to small support use and climb/suspensory behaviour (especially Figures 2, 6). Quadrupedal walk and use of horizontal supports were constantly merged together. Animalivory, leap, and understorey use formed a coherent group usually associated with another cluster composed of liana forest use, liana use, and use of vertical supports.

The use of mature forest and canopy, coupled with frugivory seems to illustrate the adaptive radiation of the largest of platyrrhines, the Atelinae (*Ateles, Lagothrix, Alouatta* from the studied sites). These platyrrhines frequently use the canopy of mainly mature high forests (Fleagle & Mittermeier, 1980; Mittermeier & van Roosmalen, 1981; Terborgh, 1983; Rosenberger & Strier, 1989; Strier, 1992). Their relatively large size allows them to move and exploit the upper forest layers of the closed canopies of mature forests, without great danger from aerial predators, in search for flush leaves and fruit (Terborgh, 1983; Strier, 1992). In effect, the ateline radiation is mainly characterised by a tendency to larger body size associated with higher rates of herbivory, and the use of suspensory and climbing patterns (Cant, 1986; Rosenberger & Strier, 1989). In these large-bodied platyrrhines, protein input is achieved through folivory, while the basic dietary regime remains frugivory, even in the highly folivorous *Alouatta* (Juillot & Sabatier, 1993) or the animalivorous *Lagothrix* (DiFiore & Rodman, 2001). As also revealed by the diagrams of French Guiana and
combined data (Figures 2, 6) frugivory was further associated with small support use and climbing/suspensory habits. For large-bodied mammals, hanging and climbing are the means for moving safely on small branches in tree crown extremities where fruit is mostly located (Cant, 1986). Hanging and climbing are modes that Atelinae frequently use not only during feeding activities but also during travel, creating shortcuts and accelerating traveling within the complex canopy that they exploit (Cant, 1986, 1992; Rosenberger & Strier, 1989). Thus, as far as the platyrhine species of the studied sites are concerned, frugivory (as well as small support use and climb/suspensory modes) along with canopy and mature forest use, form a group of strongly interrelated factors that best describe the adaptive niche occupied by the Atelinae (Rosenberger, 1992).

The consistent cluster uniting horizontal support use with quadrupedal walk illustrates the most frequent mode adopted by all platyrhines (Fleagle & Mittermeier, 1980; Garber, 1991; Youlatos 1999). Quadrupedal walk is by definition associated with very high rates of horizontal supports since more inclined supports would require different modes such as oblique or vertical ascents or descents with different kinematic characteristics. Horizontal quadrupedal walk is also considered as one of the major components of the positional behaviour of the primitive platyrhine (Ford, 1988), and this is reflected in many parts of the platyrhine postcranium despite the variety of other positional modes and postcranial adaptations (Fleagle, 1988; Rose, 1996). Even the vertically ranging smaller Callitrichinae employ frequent quadrupedal walk (Garber, 1991; Youlatos 1999), whereas the medium-sized *Cebus* or *Saimiri*, use even higher rates (Fleagle & Mittermeier, 1980; Boinski, 1989; Youlatos, 1998). The Pitheciinae also use quadrupedal walk as a major part of their positional repertoire, with the exception of *P. pithecia* (Fleagle & Meldrum, 1988; Walker, 1994, 1996; Youlatos, 1999). Even the Atelinae employ quadrupedal walk, with the most pronograde genera (*Alouatta* and *Lagothrix*) at higher rates than the more suspensory representatives (*Ateles* and *Brachyteles*) (Fleagle & Mittermeier, 1980; Cant, 1986; Cant et al., 2001). In the former Atelinae, quadrupedal walk permits stability and energy-saving traveling within the continuous parts of the closed canopies of mature forests.

The cluster linking the use of understorey, animalivory and leaping appears to best illustrate the adaptive radiation of the small Callitrichinae, especially if combined with liana forest use, liana use, and vertical support use (Garber, 1992). The secondarily acquired small body size (Ford, 1986) compels them to exploit the lower forest layers, where aerial predators are less frequent, and offer more hiding places, due to their dense architecture
(Terborgh, 1983). In parallel, their higher metabolism requires elevated rates of protein input, found mostly in insects and other invertebrates that usually abound in the dense and complex habitats of the understory (Garber, 1992). In this way, the Callitrichinae appear to exploit efficiently the parts of the forest seldom frequented by larger platyrrhines, such as the understory, forest edges, and liana forests that provide closed microhabitats enhancing camouflage and shelter, as well as available food (Mittermeier & van Roosmalen, 1981; Garber, 1992; Rosenberger, 1992). However, these habitats may also be visited by larger platyrrhines, such as Cebus or Saimiri, the diet of which comprises significant amounts of invertebrate prey (Mittermeier & van Roosmalen, 1981; Terborgh, 1983; Janson & Boinski, 1992). These habitats are usually highly discontinuous and are characterised by the abundance of large vertical trunks and other supports compelling their dwellers to frequent leaping either between vertical supports, in Cebuella and some Saguinus species, or between twigs, in other Saguinus species (Garber, 1991, 1992; Youlatos, 1999). Gummivory, employed mainly by Cebuella and Callithrix and seasonally by Saguinus, was not included in this study but is another factor contributing to the adaptive complex described above by the frequent use of claw-climbing and leaping on vertical supports in the understory (Soini, 1988; Garber, 1992; Rosenberger, 1992; Rylands, 1996). More particularly, in Yasuni, apart from the study group, most gouged trees by Cebuella were found in dense liana forests. Thus, the complex of understory use, animalivory and frequent leaping combined with vertical support use in dense liana forests describes best the adaptive radiation of the Callitrichinae.

CONCLUSION

The cluster analysis of several parameters recorded during field studies in two neotropical primate communities produced clusters of intrinsic-morphology related (body weight; locomotor mode: quadrupedal walk, climb/suspend, leaping; diet: frugivory, folivory, animalivory) and extrinsic-habitat (forest type: mature forest, liana forest; support type: lianas; support size: small, large; support orientation: horizontal, vertical) factors that appeared to illustrate parts of the adaptive radiation of New World primates.

Mature forest and canopy use combined with frugivory (further related to small support use and climb/suspend) best described the adaptive niche of the largest of platyrrhines, the Atelinae, and less the Pitheciinae. Both sub-
families were also clustered together supporting the Atelidae clade and their incipient common adaptations. On the other hand, understorey use, combined with animalivory and leaping, and further related to liana forest use and vertical support use seems to best illustrate the adaptive radiation of the small Callitrichinae. Unfortunately, the representatives of this group in the studied sites failed to group together.

In this way, intrinsic factors, such as animalivory or frugivory, leaping or quadrupedal walk interact with extrinsic factors, such as understorey or canopy use, mature forest or liana forest use, vertical supports use, to determine the major adaptive niches of the highly diversified group of platyrhines.

ACKNOWLEDGMENTS

This report could not have been drafted without the financial support of the following institutions: the "Action Spécifique Guyane" and the Laboratoire d'Anatomie Comparée (CNRS-UMR 8570) of the Muséum National d'Histoire Naturelle for field research in French Guiana; the NSF SBR-9222526 grant for field research in Ecuador. Therefore, I am extremely grateful to all the people who helped me in various ways throughout these projects: Drs. J.-P. Gasc, P. Charles-Dominique, B. de Thoisy, and B. Simmen in French Guiana; Drs. J. G. H. Cant, P. S. Rodman, L. Arcos Terén, L. Albuja V., W. Pozo R., A. DiFiore, and L. Dew in Ecuador.

La diversité des modes de locomotion des primates suggère l'interaction continue entre facteurs intrinsèques liés à la morphologie (poids corporel, régime alimentaire, modes de locomotion) et facteurs extrinsèques liés à la structure de l'habitat (architecture forestière, distribution des ressources, propriété structurale des branches utilisables). Cette diversité offre des solutions aux problèmes posés par le milieu environnant et contribue largement à l'évolution des niches adaptatives des primates, plus particulièrement des platyrhiniens du Nouveau Monde.

Ce rapport utilise des données associées à la locomotion, données de première main qui ont été collectées lors de premières rencontres et à des intervalles de 20 secondes dans deux forêts différentes, l'une en Guyane française et l'autre en Equateur. La matrice des facteurs collectés, incluant
aussi les poids corporels, concerne treize différentes espèces de platyrrhinien. Ces données sont soumises à des analyses "en clusters" de manière à évaluer les interactions entre certains facteurs intrinsèques et extrinsèques chez les platyrrhinien. Lorsque les différentes espèces sont traitées comme variables, les Atelinae et les Pithecia sont réunis dans un même "cluster", validant ainsi le clade des Atelidae. Cebuella est toujours à la base de tous les diagrammes "en clusters", tandis que Callicebus est toujours associé aux Cebinae et aux Callitrichinae. Lorsque les différents facteurs sont traités comme variables, deux diagrammes "en clusters", parmi tous ceux qui ont été calculés, sont plus ou moins cohérents. Sont ainsi regroupés en un "cluster", l'utilisation de la forêt mature, l'utilisation de la canopée, et le régime frugivore. Ce groupe de facteurs semble bien décrire la niche écologique des Atelinae. Par ailleurs, l'animalivorie, le saut, et l'utilisation du sous-bois sont aussi regroupés ensemble, généralement associés à l'utilisation de lianes, de forêts de lianes, et de supports verticaux. Ce faisceau de facteurs semble bien décrire la radiation adaptative des Callitrichinae. Ainsi nos analyses suggèrent l'existence de relations complexes entre les différents paramètres intrinsèques et extrinsèques associés à la locomotion, paramètres qui paraissent bien ici être déterminants dans les principales radiations adaptatives des platyrrhinien.

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