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THE EFFECT OF RAINFALL SEASONALITY ON THE GEOGRAPHIC DISTRIBUTION OF NEOTROPICAL PRIMATES

R. Pastor-Nieto
D. K. Williamson

Introduction

Studies carried out on the geographic distribution and ecology of New World Primates (for example, Pagel *et al.*, 1991; Ross, 1992; Rosenberger, 1992; Strier, 1992; Ford, 1994) all find that environmental variables such as temperature and rainfall have an important effect on the morphological adaptations and behavioral ecology of the platyrrhine primates.

There is a general relationship between overall body size and ecological, behavioral and physiological traits in mammals (for example, Calder, 1984; Clutton-Brock and Harvey, 1983; Eisenberg, 1981; McNab, 1987; Peters, 1983; Schmidt-Nielsen, 1984). In primates there is a consistent relationship between body size and feeding ecology (Ford and Davis, 1992). Body size by itself, therefore, is a useful predictor of a species' adaptations (Damuth and McFadden, 1990), and appears to be related to numerous life-history variables (Clutton-Brock and Harvey, 1983; Harvey and Clutton-Brock, 1985).

Platyrrhines are thought ideal for examining morphological adaptations to diet, because of their monophyletic origin, universal arboreality, and variation in food prefer-

Table 1. Mean body weights (adapted from Ford and Davis, 1992) of the platyrrhine primates, and their presence in the phytogeographic regions (Rylands *et al.*, 1995). *CCCH = Cerrado/Caatinga/Chaco; AM = Amazonia; SA = Southern Andes; MA = Middle America; NVC = Northern Venezuela-Colombia; NA = Northern Andes; AF = Atlantic forest.

Species	Male weight (g)	Female weight (g)	Mean weight (g)	Phytogeographic region
Alouatta belzebul	7270.0	5525.0	6397.5	AM
Alouatta caraya	6800.0	4605.0	5702.5	CCCH
Alouatta fusca	6175.0	4550.0	5362.5	AF
Alouatta palliata	7150.0	5350.0	6250.0	MA, NA
Alouatta pigra	11352.0	6434.0	8893.0	MA
Alouatta seniculus	7200.0	5600.0	6400.0	SA, MA, NVC
Aotus azarae	933.0	953.0	943.0	CCCH, AM
Aotus lemurinus	955.0	968.0	961.5	MA, NA
Aotus nancymae	923.0	940.0	931.5	AM
Aotus trivirgatus	920.0	950.0	935.0	AM
Ateles belzebuth	6200.0	5800.0	6000.0	AM, NVC, NA
Ateles fusciceps	8890.0	8800.0	8845.0	MA, NVC, NA
Ateles geoffroyi	8210.0	7456.0	7833.0	MA
Ateles paniscus	7460.0	9750.0	8605.0	AM
Brachyteles arachnoides	12125.0	9450.0	10787.5	AF
Cacajao calvus	3450.0	2880.0	3165.0	AM
Cacajao rubicundus	3450.0	2880.0	3165.0	AM
Cacajao melanocephalus	3450.0	2880.0	3165.0	AM
Callicebus brunneus	854.0	805.0	829.5	AM
Callicebus caligatus	1098.0	1075.0	1086.5	AM
Callicebus cinerascens	1098.0	1075.0	1086.5	AM
Callicebus cupreus	1012.0	1119.0	1065.5	AM
Callicebus donacophilus	1098.0	1075.0	1086.5	CCCCH, AM
Callicebus dubius	1098.0	1075.0	1086.5	AM
Callicebus hoffmannsi	1098.0	1075.0	1086.5	AM
Callicebus moloch	1000.0	860.0	930.0	AM
Callicebus oenanthe	1098.0	1075.0	1086.5	SA
Callicebus olallae	1098.0	1075.0	1086.5	AM
Callicebus personatus	1325.0	1285.0	1305.0	AF
Callicebus torquatus	1300.0	1307.0	1303.5	AM
Callimico goeldii	640.0	530.0	585.0	AM
Callithrix argentata	357.0	320.0	338.5	AM
Callithrix geoffroyi	290.0	190.0	240.0	AF
Callithrix humeralifera	280.0	310.0	295.0	AM
Callithrix jacchus	256.0	236.0	246.0	CCCH, AF
Cebuella pygmaea	130.0	126.0	128.0	AM
Cebus albifrons	2480.0	1814.0	2147.0	AM, SA, NVC, NA
Cebus apella	3050.0	2385.0	2717.5	CCCH, AM, SA, NVC, AF
Cebus capucinus	3868.0	2666.0	3267.0	MA, NVC, NA
Cebus olivaceus	2974.0	2395.0	2684.5	AM, NVC
Chiropotes albinasus	3020.0	2510.0	2765.0	AM
Chiropotes satanas	3100.0	2600.0	2850.0	AM
Lagothrix flavicauda	8335.0	5750.0	7042.5	SA
Lagothrix lagothricha	8335.0	5750.0	7042.5	AM
Leontopithecus chrysomelas	620.0	535.0	577.5	AF
Leontopithecus chrysopygus	614.0	557.0	585.5	AF
Leontopithecus rosalia	607.0	578.0	592.5	AF
Pithecia irrorata	2010.0	1875.0	1942.5	AM
Pithecia monachus	2795.0	1900.0	2347.5	AM
Pithecia pithecia	1732.0	1515.0	1623.5	AM
Saguinus bicolor	430.0	430.0	430.0	AM
Saguinus fuscicollis	387.0	403.0	395.0	AM
Saguinus imperator	400.0	400.0	400.0	AM
Saguinus inustus	423.0	454.0	438.5	AM
Saguinus labiatus	451.0	465.0	458.0	AM
Saguinus leucopus	490.0	490.0	490.0	AM
Saguinus midas	586.0	432.0	509.0	AM
Saguinus mystax	577.0	560.0	568.5	AM
Saguinus nigricollis	470.0	480.0	475.0	AM
Saguinus oedipus	411.0	430.0	420.5	AM
Saguinus tripartitus	423.0	454.0	438.5	AM
Saimiri boliviensis	1015.0	700.0	857.5	CCCH, AM
Saimiri oerstedi	829.0	695.0	762.0	MA
Saimiri sciureus	852.0	675.0	763.5	AM, NVC
Saimiri ustus	910.0	795.0	852.5	AM
Saimiri vanzolinii	950.0	650.0	800.0	AM

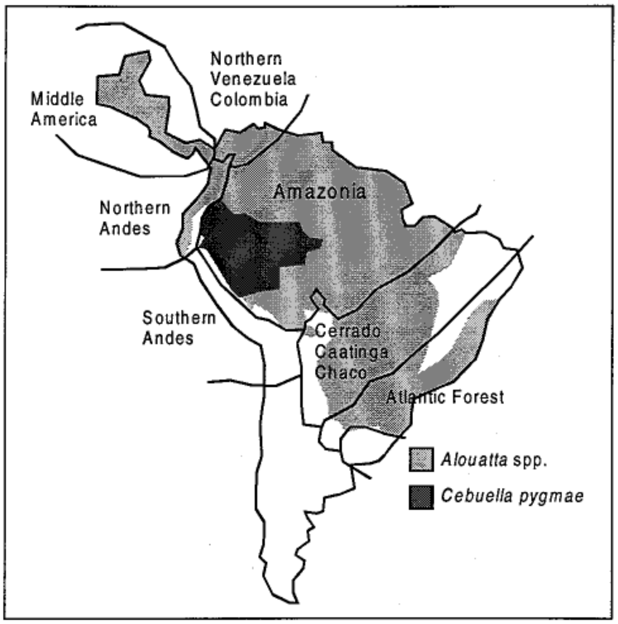

Figure 1. The geographic ranges of a large (*Alouatta*) and a small (*Cebuella*) platyrrhine, overlayed with the seven phytogeographic regions of Gentry (1982).

ences (Anapol and Lee, 1994). Differentiation of body size is a significant factor in the partitioning of platyrrhine diets and foraging strategies (for example, Temerin *et al.*, 1984; Janson and Boinski, 1992; Garber, 1992; Rosenberger and Strier, 1989; Strier, 1992).

There are currently three main hypotheses, based on ecological determinants, to explain the maximum body-weight thresholds of platyrrhines.

Terborgh and van Schaik (1987) suggested that the fruit and leafing cycles in the Neotropics are 'in-phase', therefore the species have to adapt to a seasonal environment. This leaves two options; either to specialize as folivores, or to exploit insects in periods of fruit scarcity.

Fleming *et al.* (1987) suggested that the low diversity of fleshy fruits in the Neotropics, in combination with a greater variety of fruit species, would have favored the evolution of small-bodied frugivores.

The 'brittle-branch' hypothesis (Cristoffer, 1987) proposed that the Neotropical forests had a more 'fragile' vegetation structure than its Paleotropical counterpart (Emmons and Gentry, 1983) and would have limited the evolution of large-bodied arboreal vertebrates.

All of these theories converge on one simple statement: the body size of Neotropical primates seems to be indirectly affected by climate. However, such theories do not explain the current geographical distribution of species. In this context we make two assumptions:

The larger platyrrhines, such as the atelines are distributed more evenly in the Neotropics because they are buffered against long periods of reduced food availability during the dry season (Boyce, 1979; Lindstedt and Boyce, 1985).

Table 2. Climatic variables calculated from long term records from randomly sampled weather stations (Wernstedt, 1972) for each of the phytogeographic regions (adapted from Gentry, 1982). CCCH = Cerrado/Caatinga/Chaco; AM = Amazonia; SA = Southern Andes; MA = Middle America; NVC = Northern Venezuela-Colombia; NA = Northern Andes; AF = Atlantic forest.

Phytogeographic region	Climatic variables*						
	n	T	P	RDV	Z	MO<50	P>2T
CCCH	38	21.45	1116.62	0.74	0.89	3.65	8.68
AM	30	25.08	2118.01	0.71	0.90	2.18	9.79
SA	8	23.46	1407.29	0.81	0.89	3.13	10.67
MA	20	25.73	2876.04	0.82	0.89	2.00	9.90
NVC	11	22.60	2198.11	0.79	0.90	2.55	9.36
NA	7	21.31	772.75	0.91	0.85	6.00	6.57
AF	7	21.21	1439.75	0.79	0.90	2.71	9.57
CCCH/AF	**	21.33	1302.18	0.78	0.90	3.18	9.12
CCCH/AM	**	23.26	1641.31	0.74	0.89	2.19	9.24
AF/AM	**	23.14	1778.88	0.75	0.90	2.45	9.68
AM/SA	**	23.18	1443.37	0.81	0.87	4.09	8.18
AM/NA	**	20.34	1444.83	0.82	0.89	3.71	9.90
AM/NVC	**	23.83	2158.08	0.73	0.90	2.36	9.58
NA./MA	**	23.51	1854.58	0.87	0.87	4.00	8.24
NA/NVC	**	21.95	1485.42	0.87	0.87	4.27	7.97
MA/NVC	**	234.16	2357.07	0.89	0.89	2.27	9.63

*n = number of weather stations sampled; T = mean annual temperature; P = mean annual precipitation (°C); RDV = rainfall diversity index; Z = Simpson's index of diversity; Mo<50 = number of months where mean rainfall is greater is greater than 50mm; P>2T = number of months where rainfall (mm) is greater than two times the temperature (°C).

**No sample size given since means for the overlapping sub-regions were calculated from the means of two neighboring regions.

Smaller species, such as the callitrichids, are more restricted in their geographic distribution due to their nutritional requirements (see Fleagle, 1988).

To illustrate this observation two genera were selected: a larger ateline with a wide distribution (*Alouatta* spp.), and the smallest platyrrhine genus (*Cebuella* spp.) which has a relatively restricted distribution (see Fig 1).

In this paper we test whether rainfall seasonality has an effect on the geographic distribution of platyrrhine species.

Methods

Southern and Middle America can be divided into nine phytogeographic regions (Gentry 982), which give an accurate description of Neotropical vegetation diversity. In a review of platyrrhine distribution, Rylands *et al.* (1995) listed the species occurring in seven phytogeographic regions, adapted from Gentry (1982) (see Fig. 1). They did not consider two regions, the Caribbean, because no primates occur there, and the Guyana sub-region, which is subsumed into the Amazonia region. We use the species list of Rylands *et al.* (1995) because of the detailed information on distributions provided (see Table 1).

Indexing habitat productivity and rainfall seasonality

The main climate variables influencing plant and animal life are water availability and temperature, and can be used alone to characterize vegetation patterns and plant productivity globally (Walter, 1979; Box, 1981; Le Houerou

Table 3. The smallest species for each weight category, rainfall diversity (RDV) and mean annual temperature for each of Gentry's (1982) phytogeographic regions. P values and r^2 values listed for weight category versus RDV regressions.

Phytogeographic Regions	**Body weight categories (g)**						
	< 500	**600-1000**	**1000-1500**	**1500-2500**	**2500-3300**	**3300-6400**	**6400-11000**
AM	128.0	807.0	1004.0	1732.0	3165.0	6200.0	7621.0
AF	246.0	1933.0	1004.0	*	2675.0	5362.0	10788.0
CCCH	246.0	607.0	1004.0	*	2171.5	5702.0	*
MA	420.5	955.0	*	*	3267.0	6250.0	7833.0
NVC	420.5	955.0	1065.5	*	2675.0	6400.0	8605.0
NA	490.0	955.0	1303.5	*	2675.0	*	7621.0
SA	*	955.0	*	*	2675.0	6400.0	7042.5
Diet***	I, Fr, G	I, Fr, Pr, ScFr	ScFr	*	ScFr	Fol	Fr, Fol
p values	0.001	0.01	0.04	**	0.5	0.28	0.81
r^2	0.87	0.62	0.93	**	0.28	0.20	0.06

* No species of that weight category for that particular phytogeographic region.

** No statistical tests conducted.

*** I = insectivore, Fr = frugivore, G = gummivore, ScFr = sclerocarpic-frugivore, Fol = folivore, Pr = vertebrate predator.

and Popov, 1981). However, plant productivity can be indexed indirectly in a variety of ways; plant evapotranspiration being the most accurate. Potential evapotranspiration (PET) measures the potential amount of water released into the atmosphere through plant evaporation, respiration and transpiration. In the absence of data to compute evapotranspiration, it has been suggested (Bagnouls and Guassen, 1953; Walter and Leith, 1967) that the number of months where precipitation (P), in millimeters, is less than two times the mean annual temperature (t), in degrees Celsius (P>2t) is an excellent substitute for PET. This is shown by the high correlation between the two measures (r^2= 0.938, p = 0.00; Williamson, 1997). The advantage of the P>2t index is that the data are readily available.

Seasonality of Gentry's phytogeographic regions

Gentry (1982) characterized the phytogeographic regions in terms of plant species richness, (canopy trees and lianas; ephiphytes and palmettos). Clinebell *et al.* (1995) further suggested that Neotropical tree and liana species' richness are best explained by annual rainfall and rainfall seasonality. In this analysis we characterized each of the phytogeographic regions in terms of climate, with a view to predicting habitat productivity. There is also strong evidence that insect abundance, and fruiting and leafing phenology is highly correlated with rainfall seasonality (Wolda, 1978; Terborgh, 1983; Poulin *et al.*, 1992).

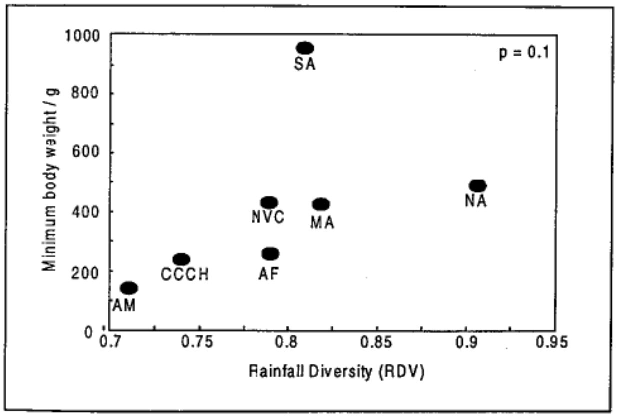

Figure 2. The smallest platyrrhine species' body weight in each of the phytogeographic regions (Gentry, 1982), regressed against rainfall diversity (RDV). CCCH = Cerrado/Caatinga/Chaco; AM = Amazonia; SA = Southern Andes; MA = Middle America; NVC = Northern Venezuela/Colombia; NA = Northern Andes; AF = Atlantic forest.

Weather stations from a worldwide climatic data source (Wernstedt, 1972) were chosen for each of the phytogeographic regions. They were selected focusing on the sampling areas in each region around known field study sites where the primates are known to live. Mean values for the climatic variables were then calculated for each of the phytogeographic regions.

Many of the primates occur in more than one phytogeographic region. These regions of overlap were considered as discrete sub-regions. Those species in the overlapping sub-regions were considered to be at the limits of their distribution, and therefore assumed to be in the most ecologically constrained part of their range. In support of this approach, it has been suggested (Strier, 1992), that one way to further distinguish between the effects of seasonality on dietary strategies (and by inference body size), is to examine data on sympatric taxa. The same climatic variables were recorded for the regions of overlap.

The following climatic variables were recorded from each of the weather stations; mean annual temperature (°C); mean annual rainfall (mm), number of months with less than 50 mm (mo<50); the number of months where mean monthly rainfall (mm) was greater than twice the mean monthly temperature (°C); and (P 2t). Two indices of rainfall diversity were calculated. The first index was Z (Simpson's index of rainfall diversity). Simpson's is an index of the proportional distribution of total rainfall across the 12 months of the year, and varies from Z = 0 (completely uneven) to Z = 1 (completely even). Simpson's index of diversity (Peet, 1974), which is derived from the species diversity literature (Magurran, 1988), has been questioned (Bronikowski and Webb, 1996; but see Williamson and Dunbar, in press), since it does not take dry months into account. There is as yet no single climatic index applicable across all habitat types. Some indices provide insufficient variance between values of the seasonality index for statistical tests; for example, when rainfall is very low or even. We used, therefore, the index of the temporal distribution (RDV) of rainfall (Williamson, 1997). RDV is calculated by finding the difference between all possible pair-wise comparisons of the 12 mean monthly rainfall values, then finding the mean of these differences. This statistic is based on the exact randomization test (Sokal and Rohlf, 1981; p.788). RDV records the opposite of Z, a high value indicates a more seasonal environment, a low value a less seasonal environment. The climate data for the regions and overlapping regions is shown in Table 2.

Body weight categories

We divided the platyrrhines into body weight categories that would reflect finer-grained dietary adaptations, since body size and dietary quality are related (Fleagle, 1988; Anapol and Lee, 1994). To test whether rainfall seasonality has an effect on the geographic distribution of platyrrhines, the smallest species was chosen for each of the seven body weight categories, for each of Gentry's regions (Table 3). The smallest species were selected since they would be expected to be more constrained in their distribution, and because small species they are less able to buffer themselves against unpredictable food availability in fluctuating environments.

Results

Initial diagnostic Spearman rank correlations showed RDV to be the only climatic variable significantly correlated with body weight, so only those results will be presented here.

Table 4. Genera inhabiting each phytogeographic region, and those occupying regions overlapping phytogeographic regions. MA = Middle America; NA = Northern Andes; NVC = Northern Venezuela-Colombia; SA = Southern Andes; AM = Amazonia; AF = Atlantic Forest; CCCH = Cerrado/Caatinga/Chaco.

Phytogeographic region	Genera
MA	*Saguinus, Aotus, Saimiri, Cebus, Alouatta, Ateles*
NA	*Saguinus, Aotus, Callicebus, Cebus, Alouatta, Ateles, Lagothrix*
NVC	*Saguinus, Aotus, Callicebus, Saimiri, Cebus, Alouatta, Lagothrix*
SA	*Aotus, Callicebus, Cebus, Alouatta, Lagothrix*
AM	*Cebuella, Callithrix, Saguinus, Aotus, Callicebus, Saimiri, Cebus, Pithecia, Chiropotes, Cacajao, Alouatta, Ateles, Lagothrix*
AF	*Callithrix, Leontopithecus, Callicebus, Cebus, Alouatta, Brachyteles*
CCCH	*Callithrix, Aotus, Callicebus, Cebus, Alouatta*
Overlapping regions	
CCCH/AF	*Callithrix, Callicebus, Cebus, Alouatta*
CCCH/AM	*Callithrix, Aotus, Callicebus, Cebus, Alouatta*
AF/AM	*Callithrix, Callicebus, Cebus, Alouatta*
AM/NA	*Saguinus, Aotus, Callicebus, Saimiri, Cebus, Alouatta, Ateles*
AM/SA	*Aotus, Callicebus, Cebus, Alouatta, Lagothrix*
AM/NVC	*Saguinus, Aotus, Saimiri, Cebus, Alouatta, Ateles*
NA/MA	*Saguinus, Aotus, Cebus, Alouatta*
NA/NVC	*Saguinus, Aotus, Callicebus, Cebus, Alouatta, Ateles*
NA/NVC	*Saguinus, Aotus, Saimiri, Cebus, Alouatta, Ateles*

Body weight relationships with climate

The body weight of the smallest species in each of the seven phytogeographic regions was positively correlated with RDV ($r^2 = 0.70$, $F = 2.19$, $p = 0.01$), (Fig. 2). The regions containing the smallest species had the most even spread of rainfall (low RDV, or non-seasonal environments).

Body weight categories were regressed against RDV (Table 3, Fig. 3). As body weight increases, the significance level of the regression slope decreases (Table 3), being non-significant from the 2300 g category and upwards (Figs. 3: D, E. and F.). The most highly significant regression is that for the category <500g ($r^2 = 0.87$, $p = 0.001$). This corresponds to "Kay's threshold" (Kay, 1975) which defines the boundary between insectivorous (<500g) and folivorous primates (>500g).

Discussion

This study suggests that rainfall seasonality acts as a selective force on the distribution of body weights in Neotropical primates. The results of this study summarize what has already been suggested by other authors (for example, Cristoffer, 1987; Ross, 1992; Kinzey, 1994), that the adaptive morphological changes in body size are affected by environmental factors. In this paper we have analyzed in detail how environmental factors characterize rainfall seasonality and hence habitat productivity in each of Gentry's phytogeographic regions.

The most important result presented in this paper is the very significant effect that rainfall seasonality has on the geographic boundaries of the smallest species and how, in very seasonal habitats, only larger platyrrhines are found. Species' with body weights of less than 500g can only be distributed in the Amazonian region, which has a tendency to be less seasonal, favoring year-round food availability.

The smallest body weight category plotted against rainfall seasonality (RDV) (Fig. 3: A; Table 3), has the most highly significant regression slope of all the body weight categories ($r^2 = 0.87$, $p = 0.001$). This result corresponds to "Kay's threshold" (Kay 1975, 1984), and applies to the entire Order Primates. Smaller animals require a higher protein content in their diet, and therefore have a higher

Table 5. Mean body weights for each of the platyrrhine genera.

Genus	Mean weight (g)
Alouatta	6500.92
Aotus	942.75
Ateles	7820.75
Brachyteles	10787.5
Cacajao	3165
Callicebus	1086.58
Callimico	585
Callithrix	279.88
Cebuella	128
Cebus	2704
Chiropotes	2807.5
Lagothrix	7042.5
Leontopithecus	585.17

basal metabolic rate (BMR), and consequently higher energetic needs (reviewed in Ford and Davis, 1992). Kay (1984) stated that no primarily insectivorous primates (>30-40% of their diet composed of insects) would weigh more than 700g. Significantly, this body weight threshold also correlates with twinning and monogamy (Dunbar, 1995a, 1995b), features only found in callitrichids. On the other hand, for the middle-sized and larger platyrrhines (>1 kg), troop fragmentation appears to be a facultative adjustment to food scarcity (Kinzey and Cunningham, 1984).

Rosenberger (1992) suggested that small and large platyrrhines have overcome the problem of seasonality in two different ways:

1. Smaller species, which require a high energy diet, will shift to alternative food resources (e.g., gums or insects) in the dry season when fruit is scarce. For example, *Saguinus fuscicollis* switches from fruit to predominantly nectar in the dry season (Terborgh and Stern, 1987), and thus avoids competition with larger primates by feeding on specialized resources (Garber, 1992). Alternatively Peres (1989) suggests, that small species switch to different feeding locations, where insects are more likely to be concentrated in the dry season, such as gumlicks and knotholes. We need to be cautious, therefore, in suggesting that resources for the smaller primates are fewer in the dry season.

2. Larger platyrrhine primates have solved the problem of seasonality with folivory. Leaves are available year-round, although they are a low-quality food resource that requires special adaptations to overcome the problems of its digestion (Rosenberger, 1992). Large body size, an adaptation

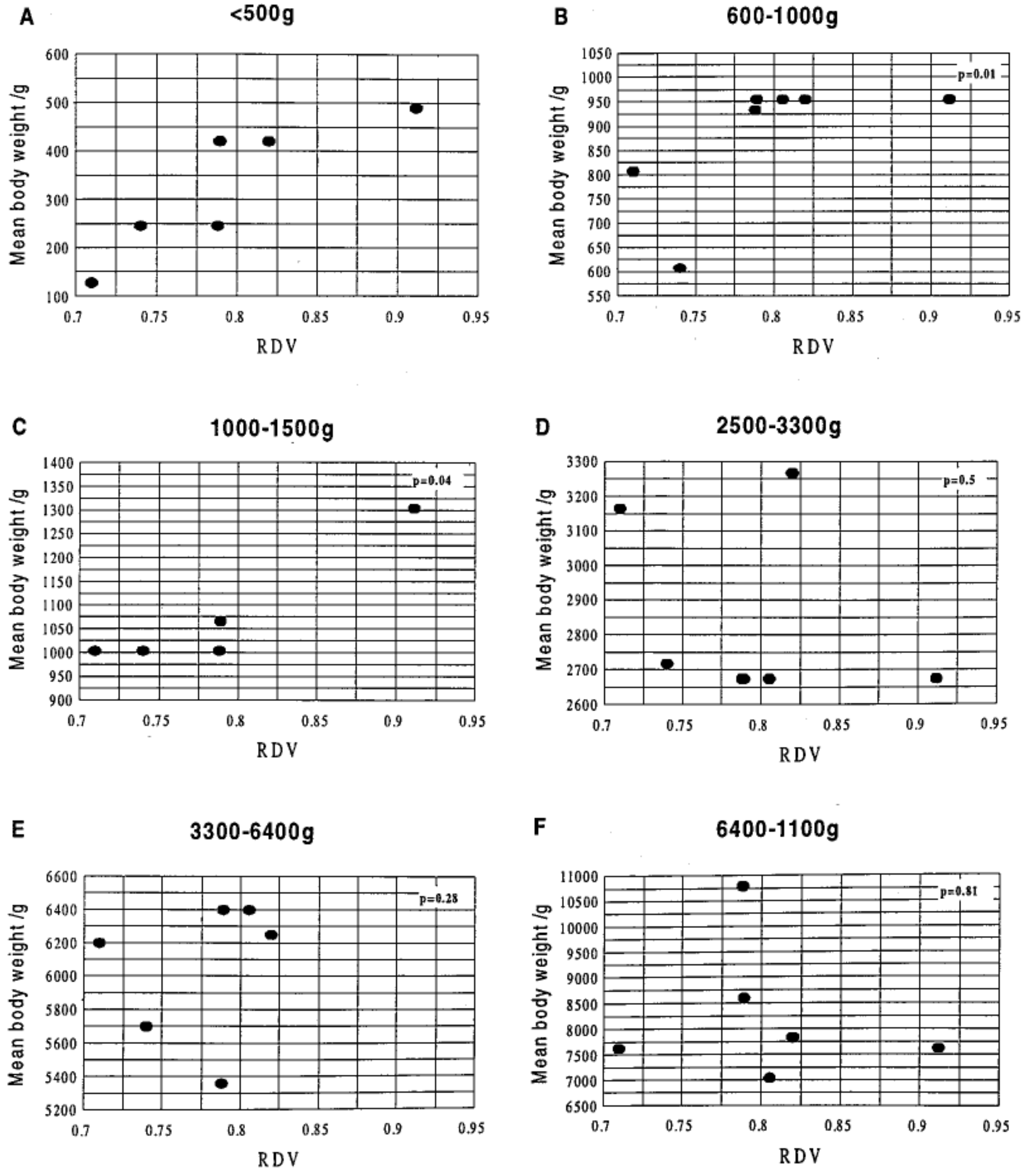

Figure 3. The smallest platyrrhine primate in each of the body weight categories (see Table 3) in each phytogeographic region against rainfall diversity (RDV). **A.** less than 500 g (dotted line indicates Kay's threshold); **B.** 600-1000 g; **C.** 1000-1500 g; **D.** 2500-3300 g; **E.** 3300-6400 g; **F.** 6400-11000 g.

to folivory, buffers against harsh seasonal habitats. This is supported by recent discoveries of giant extinct pitheciines (Hartwig, 1995; Hartwig and Cartelle, 1996), weighing as much as 25 kg. Their extreme large size may be an adaptation to competition for resources in a harsh habitat, brought on by climate changes in the Pleistocene.

Low rainfall seasonality habitats evidently permit the survival of a wider variety of primate species, but there is a need to understand better the environmental factors that underlie the biogeographic distribution of species if we are to devise effective conservation strategies.

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R. Pastor-Nieto, Coordinador Proyecto Hampolol, Universidad Autonoma de Campeche, ECOMAT, Avenida Universidad s/n, Campeche, Campeche, México, and **D. K. Williamson**, Hominid Palaeontology Research Group, Department of Human Anatomy and Cell Biology, University of Liverpoool, New Medical School, Ashton Street, Liverpoool L69 3GE, UK.

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THE SQUIRREL MONKEY BREEDING COLONY OF THE PASTEUR INSTITUTE, CAYENNE, FRENCH GUIANA

Benoît de Thoisy
Hugues Contamin

Introduction

Squirrel monkeys, especially *Saimiri sciureus* and *S. boliviensis*, are animal models widely used in biomedical research; mainly in pharmacology, toxicology, cancerology, nutrition, cardiovascular diseases and neurology (Mittermeier *et al.*, 1994). Numerous captive breeding colonies have been established in different parts of the world. However, reproduction of captive squirrel monkeys is often inconsistent, giving rise to disappointing breeding results. The aim of this article is to briefly present the 15-year-old colony of the Pasteur Institute of French Guiana, emphasizing efforts to ensure the well-being of the monkeys and, being a biomedical research institution, the results obtained using this non-human primate model.

In 1978, The Pasteur Institute of French Guiana, belonging to a network of international Pasteur Institutes, decided to initiate a long-term research program on human malaria. Although not the natural host of either *Plasmodium vivax* or *P. falciparum, Saimiri sciureus* was chosen as a model because it is sensitive to experimental infection (Gysin, 1991). Moreover, squirrel monkeys naturally