

Seasonal Reproduction in Neotropical Rainforest Mammals

G rard Dubost* and Olivier Henry

Mus um national d'Histoire naturelle, EGB-UMR 7204, M nagerie du Jardin des Plantes, 57 rue Cuvier, 75231 Paris C dex 05, France

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G rard Dubost, and Olivier Henry (2017) Seasonal changes in tropical forests have been documented in dry and semi-deciduous forests, but not in evergreen ones. Owing to its high level of annual rainfall, French Guiana is considered to be a rainy region, despite a pronounced dry season. French Guiana is therefore appropriate for studying the impact of the dry season on the phenology of rainforest animals. For this purpose, the reproductive characteristics of six terrestrial mammals of the French Guiana rainforest were studied during the four main seasons of the year. Reproduction was more or less continuous in both sexes of all species. Seasonality was not very pronounced and the species were not synchronised, except in terms of births. In all species, the minimum number of litters occurred between August and October. Furthermore, the seasonal birth percentages appeared to be linked to environmental factors such as rainfall and fruiting trees, and to diet as well: the more the diet of one species was composed of fruits, the more seasonal its litters were. Thus, like in many other regions worldwide, most births occur during the most favourable seasons for raising young in this rainforest. This signifies that even in this seemingly aseasonal region, the reproduction of mammals is mainly regulated by environmental factors at the time of birth.

Key words: French Guiana, Rainforest, Seasonal reproduction, Terrestrial mammals.

BACKGROUND

Like elsewhere, tropical forest animals undergo seasonal changes in reproduction, particularly during the dry season (Butynski 1988; Van Schaik et al. 1993; Nicolas and Colyn 2003). Births can then come to a halt for several months (Butynski 1988; Goldizen et al. 1988). This phenomenon has been recognised for a long time (Davis 1945) and documented in semi-deciduous and dry tropical forests but not in evergreen ones. According to the criteria used by Van Schaik et al. (1993), French Guiana must be considered as an aseasonal rainy region. However, its main dry season is well pronounced (Gayot et al. 2004). Thus, French Guiana is appropriate for studying the impact of the dry season on the phenology of rainforest animals. For this purpose, we analysed the reproduction of several sympatric terrestrial mammals of different sizes. As far as we know,

no study of a guild of tropical rainforest mammals has ever been undertaken, except in some primates and small rodents. As a consequence of the marked cycle of rainfall and fruit production in French Guiana (Dubost et al. 2005), we assumed that seasonal variations occurred in the reproductive patterns of these species, and that they were not the same for all species as a result of their differences in body mass, that is especially in terms of gestation period and metabolic needs. Thus, they would be more pronounced in large than in small species. Finally, we also assumed that these variations were linked to climatic factors, ground resources or species diet.

MATERIALS AND METHODS

The species studied were, in order of increasing body mass, five rodents and

*Correspondence: E-mail: gerard.dubost@mnhn.fr

one artiodactyl: the small murid *Hylaeamys megacephalus* (Fischer, 1814; formerly *Oryzomys capito velutinus*; 20-70 g); the spiny rat *Proechimys cuvieri* (Petter, 1978; 200-500 g); the acouchy *Myoprocta acouchy* (Erxleben, 1777; 0.85-1.45 kg); the agouti *Dasyprocta leporina* (L. 1758; 3-5.9 kg); the paca *Agouti paca* (L. 1766; 5.6-9.8 kg); and the collared peccary *Tayassu tajacu* (L. 1758; 18-26 kg).

In French Guiana, rainfall is the most variable and the most important climatic factor (Dubost et al. 2005). The annual rainfall is 1,700-3,800 mm (2,895 mm on average), with abundant rains (> 200 mm/month) between December and July, and a minimum (< 160 mm/month) from August to November (1981-1991: data from Météo France; Fig. 1). Another major determinant for the biology of the animals is the availability of food. Since all the species studied were frugivorous, fruit production was estimated by counting the number of fruiting trees per km of trail on a monthly basis for three consecutive years (1980-1982: Gayot et al. 2004). Unlike rains, fruit production is unimodal, which is somewhat unusual in the neotropics (Van Schaik et al. 1993). As shown in figure 1, rainfall and fruit production vary greatly during the year, and their distribution differs from a homogeneous distribution among the seasons (Gayot et al. 2004). Although the minima are the same, there is no correlation between the two phenomena. According to Henry (1994) and Dubost and Henry (2006), the seasonal variations of diet items distinguishable in the stomach contents (pulp, seeds, animal matter, shells/stems, leaves) were not pronounced (Table

1). They were significant only in the three main food categories: pulp in the smallest species and in the two largest rodents, seeds in the three largest rodents, and animal matter in the smallest species.

Reproductive organs of these species were collected over many years (most of them between 1979 and 1991) from local hunters throughout French Guiana (2-6°N, 52-54°W), except for the two small rodents that were captured over three consecutive years (1989-1991) at only one site (Paracou: 5°15'N, 52°55'W). In total, this represented from 36 to more than 200 individuals per species. We estimated the percentage of mature males (by direct observation under the microscope of spermatozoa present in the cauda epididymis), the percentage of mature females that were pregnant (from embryos in utero), and the percentage of beginning of gestation and of litters (observed or calculated on the basis of embryo size, according to the gestation period) over the yearly total. We did not take the litter size into account.

Because samples were sometimes too small for an analysis at a monthly level, data were grouped into four seasons of three months each, according to the evolution of rainfall and fructification (Dubost et al. 2005). Distributions of percentages among seasons were compared to a homogeneous distribution by the χ^2 -test, using base data. Due to the small number of species (6), and seasons (4) distinguished, correlations were established using the Spearman rank correlation coefficient r_s (Siegel and Castellan 1988).

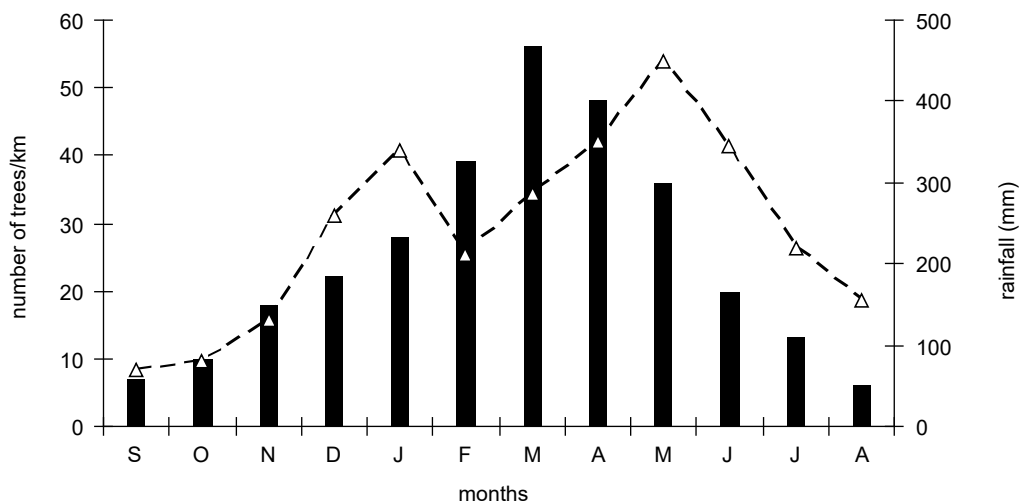


Fig. 1. Rainfall (1981-1991; curve, in mm) and number of fruiting trees per km of trail (1980-1982; black bars) according to the month (from Gayot et al. 2004).

RESULTS

Males with spermatozoa

Subadult and adult males were reproductive in every season. The yearly percentage of males with spermatozoa in the cauda epididymis varied between 47 and 74%, without significant differences between species. Seasonal variations were significant for all of them (from $\chi^2_3 = 10.81$, $p < 0.02$ to $\chi^2_3 = 29.28$, $p < 0.001$; Table 2). However, the maximum and minimum greatly differed among the species that were therefore not synchronised, except *M. acouchy* with *D. leporina* ($r_s = 1.000$, $p = 0.05$).

Beginning of gestation

The beginning of gestation occurred in all seasons, with comparable yearly percentages in species (22-26%). Contrary to males, the seasonal variations were not pronounced, except in *M. acouchy* ($\chi^2_3 = 43.12$, $p < 0.001$; Table 2). There was no synchronisation between the species, with the exception of *D. leporina* with *T. tajacu* ($r_s = 1.000$, $p = 0.05$). The beginning of gestation was correlated with the percentage of males with spermatozoa only in *P. cuvieri* and *M. acouchy* ($r_s = 1.000$, $p = 0.05$).

Table 1. Annual (median of the four seasons) and seasonal percentages (in dry mass) of different food categories in the stomach contents of the species. In brackets, number of individuals studied per species. F-Ap: February-April; M-Jy: May-July; A-O: August-October; N-J: November-January. Seasonal variations: ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: non significant. From Henry 1994, Dubost and Henry 2006, modified

| | | <i>H. megacephalus</i> (36) | <i>P. cuvieri</i> (36) | <i>M. acouchy</i> (53) | <i>D. leporina</i> (36) | <i>A. paca</i> (57) | <i>T. tajacu</i> (36) |
|---------------|---------------------|--------------------------------|---------------------------|---------------------------|----------------------------|------------------------|--------------------------|
| Pulp | Year | 34.37 | 50.13 | 68.85 | 41.70 | 46.30 | 14.43 |
| | F-Ap | 71.97 | 61.57 | 64.80 | 51.07 | 48.90 | 30.27 |
| | M-Jy | 32.23 | 41.10 | 94.70 | 32.33 | 65.60 | 11.57 |
| | A-O | 15.43 | 30.50 | 60.20 | 9.50 | 43.70 | 9.57 |
| | N-J | 36.50 | 59.17 | 72.90 | 57.97 | 21.70 | 17.30 |
| | Seasonal variations | *** | ns | ns | *** | ** | ns |
| Seeds | Year | 6.23 | 12.77 | 15.00 | 42.97 | 14.30 | 44.63 |
| | F-Ap | 5.37 | 10.67 | 22.90 | 32.50 | 17.60 | 38.60 |
| | M-Jy | 7.10 | 12.87 | 0.07 | 53.43 | 5.40 | 52.80 |
| | A-O | 10.43 | 20.53 | 23.10 | 68.63 | 11.00 | 50.67 |
| | N-J | 3.17 | 12.67 | 7.10 | 29.97 | 25.30 | 34.60 |
| | Seasonal variations | ns | ns | *** | * | * | ns |
| Animal matter | Year | 59.85 | 34.93 | 0.02 | 8.73 | 0.01 | 10.93 |
| | F-Ap | 22.00 | 27.23 | 0.01 | 7.00 | 0.01 | 9.23 |
| | M-Jy | 59.87 | 42.63 | 0.04 | 10.47 | 0.01 | 13.17 |
| | A-O | 73.57 | 48.60 | 0.01 | 12.37 | 0.01 | 12.63 |
| | N-J | 59.83 | 24.67 | 0.02 | 6.37 | 0.01 | 7.37 |
| | Seasonal variations | *** | ns | ns | ns | ns | ns |
| Shells/stems | Year | ~ 0.00 | 0.25 | 3.00 | 4.17 | 11.95 | 17.50 |
| | F-Ap | 0.00 | 0.40 | 3.81 | 7.90 | 15.60 | 12.90 |
| | M-Jy | 0.00 | 0.00 | 2.82 | 2.57 | 16.20 | 12.77 |
| | A-O | 0.00 | 0.10 | 2.33 | 5.40 | 7.90 | 22.10 |
| | N-J | 0.00 | 2.43 | 3.17 | 2.93 | 8.30 | 29.10 |
| | Seasonal variations | ns | ns | ns | ns | ns | ns |
| Leaves | Year | 0.53 | 0.67 | 0.01 | 2.15 | 1.10 | 8.80 |
| | F-Ap | 0.50 | 0.10 | 0.01 | 1.53 | 0.79 | 8.90 |
| | M-Jy | 0.90 | 3.37 | 0.01 | 1.20 | 0.32 | 8.70 |
| | A-O | 0.57 | 0.27 | 0.07 | 2.97 | 1.40 | 4.97 |
| | N-J | 0.50 | 1.07 | 0.01 | 2.77 | 3.10 | 11.50 |
| | Seasonal variations | ns | ns | ns | ns | ns | ns |

Pregnant females

Pregnant females were encountered throughout the year, with yearly percentages varying between 34 and 69%. *A. paca* showed the highest percentage (69%), followed by *H. megacephalus* (61%). *M. acouchy* had the lowest one, but differences between species were not significant. Seasonal variations were significant (from $\chi^2_3 = 7.75, p \sim 0.05$ to $\chi^2_3 = 70.22, p < 0.001$), except in the above two species that had the highest percentages (Table 2). In all species, females were the least often pregnant between May and October. However, they were not synchronised, except *D. leporina* with *A. paca* ($r_s = 1.000, p = 0.05$).

Births

Births showed the same yearly percentages

as at the beginning of gestation. They took place in every season but they were less numerous between August and October in all species. The seasonal variations were significant in *M. acouchy*, *D. leporina* and *A. paca* ($\chi^2_3 = 43.13, p < 0.001$; $\chi^2_3 = 8.4, p < 0.05$; $\chi^2_3 = 11.95, p < 0.01$, respectively), even with a total halt in births in the former species. In the other three species, the decrease in the number of litters was less pronounced (Table 2). Although the minimum number of litters occurred at the same period in all species, three groups could be distinguished among them (Fig. 2b): (1) the two small species that showed the lowest seasonal differences in litter percentages (7.7-8.2%) and that were synchronised ($r_s = 1.000, p = 0.05$); (2) the three largest species with medium seasonal differences (24.2-30.0%) and that were also synchronised ($r_s = 1.000, p = 0.05$); and (3) *M. acouchy* with the greatest difference (55.5%).

Table 2. Annual (median of the four seasons) and seasonal percentages of males with spermatozoa in the cauda epididymis, beginning of gestation, pregnant females, and births in the species. In brackets, number of individuals studied per species. F-Ap: February-April; M-Jy: May-July; A-O: August-October; N-J: November-January. Seasonal variations: ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: non significant

| | | <i>H. megacephalus</i> | <i>P. cuvieri</i> | <i>M. acouchy</i> | <i>D. leporina</i> | <i>A. paca</i> | <i>T. tajacu</i> |
|-------------------------|---------------------|------------------------|-------------------|-------------------|--------------------|----------------|------------------|
| Gestation period (days) | | 26 | 65 | 99 | 110 | 118 | 150 |
| Males with spermatozoa | Year | 67.83 (119) | 73.34 (93) | 55.00 (27) | 73.67 (86) | 55.00 (44) | 47.50 (61) |
| | F-Ap | 81.33 | 100.00 | 50.00 | 60.00 | 66.67 | 19.33 |
| | M-Jy | 83.33 | 33.33 | 14.29 | 30.00 | 50.00 | 66.67 |
| | A-O | 40.33 | 50.00 | 63.64 | 100.00 | 60.00 | 81.67 |
| | N-J | 54.33 | 96.67 | 60.00 | 87.33 | 25.00 | 28.33 |
| | Seasonal variations | * | *** | *** | *** | ** | *** |
| Beginning of gestation | Year | 26.15 (74) | 24.65 (83) | 22.22 (9) | 25.25 (100) | 22.86 (35) | 21.85 (66) |
| | F-Ap | 28.00 | 33.10 | 11.11 | 14.00 | 25.72 | 18.70 |
| | M-Jy | 27.50 | 17.60 | 0.00 | 24.80 | 14.28 | 20.80 |
| | A-O | 24.80 | 21.00 | 55.55 | 35.50 | 20.00 | 37.60 |
| | N-J | 19.70 | 28.30 | 33.33 | 25.70 | 39.99 | 22.90 |
| | Seasonal variations | ns | ns | *** | ns | ns | ns |
| Pregnant females | Year | 60.77 (35) | 53.85 (30) | 34.72 (36) | 41.24 (35) | 68.63 (44) | 47.33 (29) |
| | F-Ap | 58.26 | 81.82 | 25.00 | 42.36 | 70.59 | 50.73 |
| | M-Jy | 54.58 | 58.66 | 0.00 | 28.30 | 50.00 | 43.93 |
| | A-O | 64.73 | 39.48 | 44.44 | 40.11 | 66.67 | 31.36 |
| | N-J | 63.27 | 49.04 | 100.00 | 83.77 | 88.89 | 69.61 |
| | Seasonal variations | ns | * | *** | *** | ns | * |
| Births | Year | 25.00 (58) | 25.78 (109) | 22.22 (9) | 25.68 (121) | 26.43 (35) | 21.73 (89) |
| | F-Ap | 25.65 | 27.20 | 33.33 | 37.85 | 38.57 | 40.35 |
| | M-Jy | 28.85 | 28.30 | 11.11 | 27.45 | 31.43 | 22.55 |
| | A-O | 21.15 | 20.15 | 0.00 | 10.80 | 8.57 | 16.20 |
| | N-J | 24.35 | 24.35 | 55.56 | 23.90 | 21.43 | 20.90 |
| | Seasonal variations | ns | ns | *** | * | ** | ns |

Relationship between reproduction and rainfall or number of fruiting trees

A direct relationship between the percentage of males with spermatozoa and rainfall could only be established in *H. megacephalus* ($r_s = 1.000$, $p = 0.05$). No other relationship was found, particularly with the number of fruiting trees.

No relationship was found concerning the beginning of gestation in the two small species. Unexpectedly, an inverse correlation appeared with the quantity of rains and fruiting trees in the two medium-sized species, and this opposition was the most obvious when data were compared on a monthly basis ($r_s = -0.705$, $p \sim 0.01$ and $r_s = -0.600$, $p < 0.05$, respectively in *M. acouchy*;

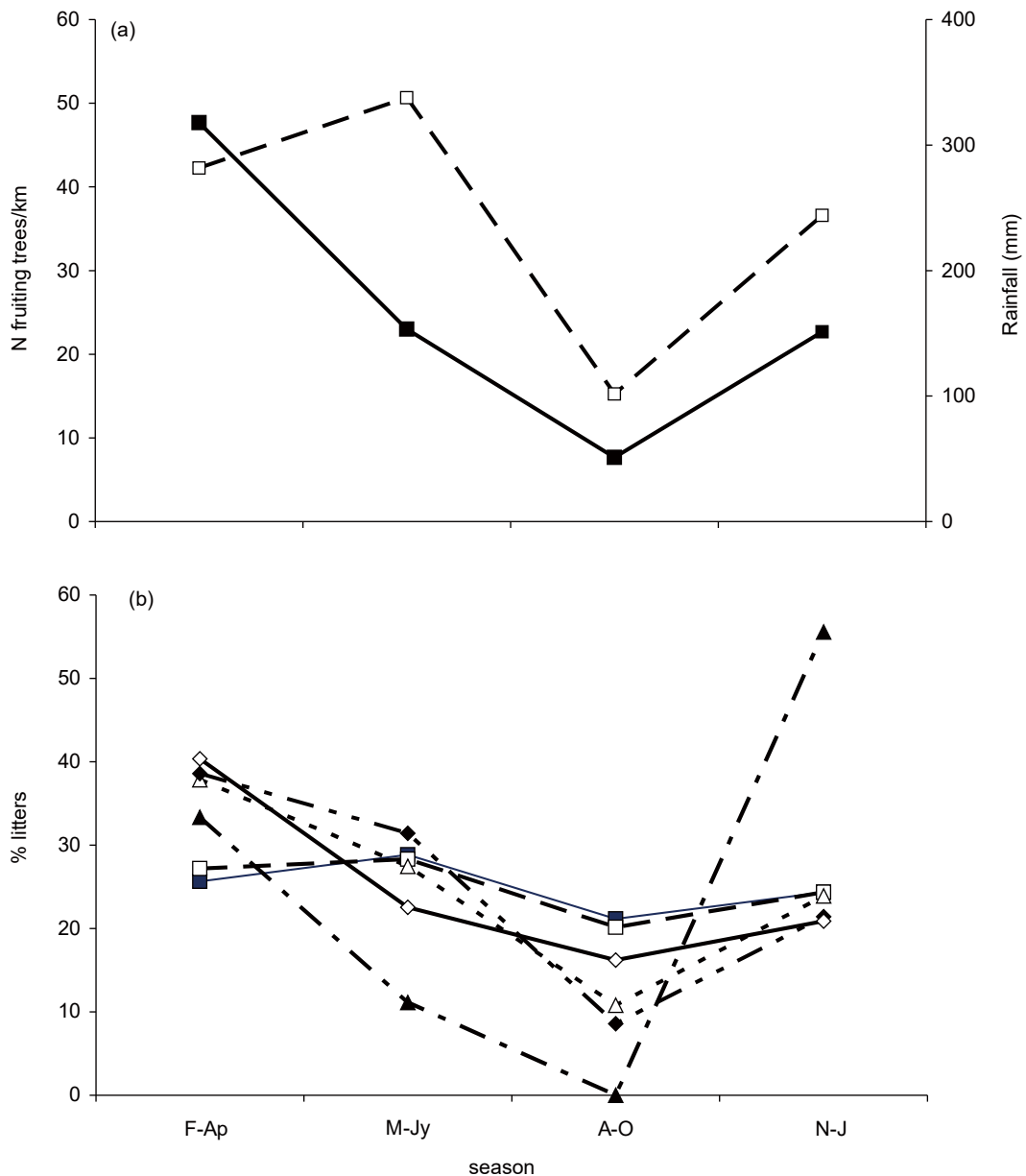


Fig. 2. (a) Average monthly number of fruiting trees per km (continuous line) and average monthly rainfall (in mm; dashed line); (b) Percentage of litters over the yearly total, according to the season. Number of pregnant females -- 35, 30, 36, 35, 44, 29 -- and number of litters -- 58, 109, 9, 121, 35, 89 -- in *H. megacephalus*, *P. cuvieri*, *M. acouchy*, *D. leporina*, *A. paca* and *T. tajacu*, respectively. *H. megacephalus* (black squares), *P. cuvieri* (white squares), *M. acouchy* (black triangles), *D. leporina* (white triangles), *A. paca* (black diamonds), and *T. tajacu* (white diamonds). F-Ap: February-April; M-Jy: May-July; A-O: August-October; N-J: November-January.

$r_s = -0.713, p < 0.01$ and $r_s = -0.619, p < 0.05$, respectively in *D. leporina*). The same inverse relationship also occurred in the two largest species, but it was significant only with the rains in *A. paca* ($r_s = -0.538, p < 0.05$) and with the fruiting trees in *T. tajacu* ($r_s = -0.745, p < 0.01$).

No relationship was found with regard to the percentage of pregnant females, except in *P. cuvieri* with the number of fruiting trees ($r_s = 1.000, p = 0.05$).

On the contrary (Fig. 2a-b), the percentage of litters varied with rainfall in the two small species ($r_s = 1.000, p = 0.05$). This was probably the same concerning the three largest species ($r_s = 0.943, p \sim 0.05$). Inversely, the percentage of litters varied with the number of fruiting trees in the latter three species ($r_s = 1.000, p = 0.05$), and this was probably also the case in the two small species ($r_s = 0.943, p \sim 0.05$). No correlation occurred in *M. acouchy*.

Relationship between reproduction and diet

There was no relationship between the seasonal percentage of males with spermatozoa and diet, except with the percentage of leaves in *D. leporina* ($r_s = 1.000, p = 0.05$). There was no relationship concerning the beginning of gestation, except in *A. paca* with seeds ($r_s = 1.000, p = 0.05$). Likewise, there was no relationship between the percentage of pregnant females and diet, except in *A. paca* with seeds and in *T. tajacu* with

leaves ($r_s = 1.000, p = 0.05$). Finally, there was no relationship between the percentage of litters and diet. However (Fig. 3), the more the diet of one species was composed of fruits (pulp + seeds), the more seasonal its litters were ($r_s = 0.829, p = 0.05$). Inversely, the species that consumed the most animal matter showed the smallest seasonal variations in litter percentage: *H. megacephalus*, *P. cuvieri* and *T. tajacu*.

DISCUSSION

Globally, the reproduction of the species studied appeared to be more or less continuous in both sexes, as is the case for many mammals in comparable regions (Dubost 1968; Dubost and Feer 1992; Gottdenker and Bodmer 1998). This is consistent with the high level of annual rainfall in French Guiana. In percentages of individuals with spermatozoa in the cauda epididymis, males showed asynchronous but significant specific cycles, as was observed for the testicle mass in several species, including *T. tajacu* (Henry 1994). Asynchronous cycles were also observed at the beginning of gestation. However, males and females appeared to be in phase in only two species. This was due to the considerable seasonal variations that occurred in males, unlike females. Nevertheless, this apparently had little effect since the percentage of males with spermatozoa exceeded 50% in more than

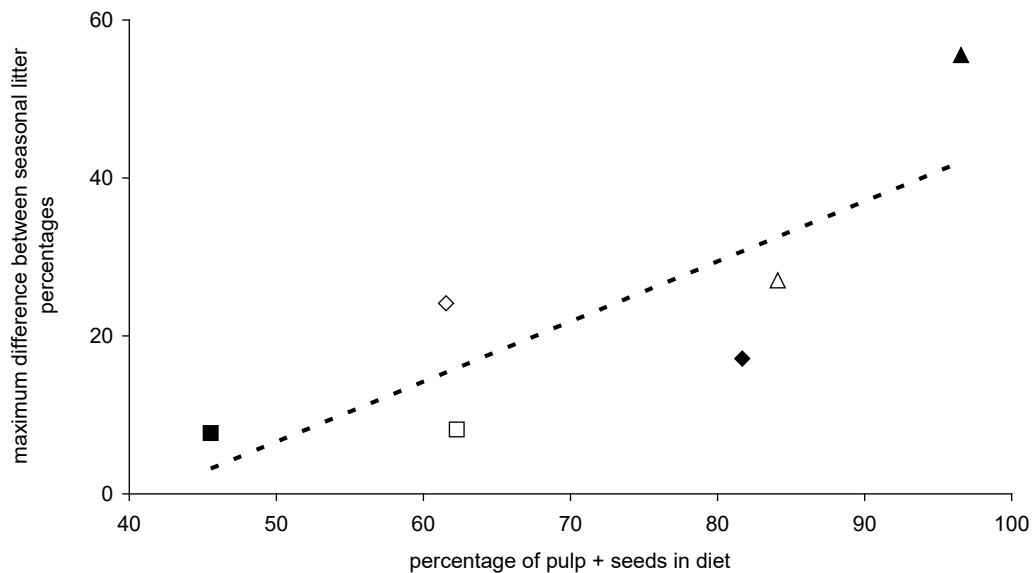


Fig. 3. Relationship between percentage of pulp + seeds in the diets and maximum difference between seasonal litter percentages. Same legend as for figure 2.

two-thirds of the cases. The minimum gestation percentage occurred between May and October in all species. For them, seasonal variations were often moderate, although significant, in the four species with the lowest gestation percentages.

The preceding increase in seasonality from the beginning of gestation to pregnant females was even more pronounced in females that gave birth, since a minimum number of litters occurred between August and October in all species, even leading to a complete halt in *M. acouchy*.

As predicted, seasonal variations in the reproductive parameters appeared in all species. They were significant in the majority or in all of them, except for the beginning of gestation. They also occurred at different periods according to the species, except for the litters. However, contrary to what was expected, they were not more pronounced in the large than in the small species. On this point, *M. acouchy*, a medium-sized species, always revealed the highest seasonal differences.

The percentages of males with spermatozoa, of beginning of gestation and pregnant females were not directly correlated with rainfall or number of fruiting trees, except in two cases in the two small species. This contradicts our initial hypothesis. Furthermore, the fact that the beginning of gestation varied inversely with the number of fruiting trees in the four largest species is difficult to explain. Indeed, its maximum occurs five months after the maximum fruit production, which apparently does not correspond to the delay necessary for the females to regain the energy to reinitiate their reproduction. However, a lack of correspondence between beginning of gestation and availability in fruit resources also appears in frugivorous ruminants of other continents (Dubost and Feer 1992).

On the contrary, in all of the species except *M. acouchy*, seasonal variations in litters were correlated both with rainfall and fructification and, more particularly, with rainfall in the two small rodents, as is the case for small rodents and shrews in other regions (Davis 1945; Southern and Hook 1963; Dieterlen 1967; Dubost 1968; Nicolas and Colyn 2003; Nicolas et al. 2005), and with fructification in the three largest ones, as in other mammals of similar size (Butynski 1988; Goldizen et al. 1988; Dubost and Feer 1992). This could signify that a link exists between the seasonality of litters in the species and the availability of their main food.

In fact, insects that were consumed in large

quantities by the two small rodents are particularly abundant in the field during the rainy season (Tanaka 2000; Trapero-Quintana and Reyes-Tur 2010; Valtonen et al. 2013). This is also the case for many bird species in the lowland forests of West Cameroon, Uganda, and Panama (Serle 1981; Dranzoa 2001; Wikelski et al. 2003). In Central Amazonia, where the quantity and pattern of rainfall are comparable to those of French Guiana, the maximum reproduction of birds took place between the middle of the dry season and the beginning of the main rainy season (Stouffer et al. 2013). However, in regions where rains are less abundant and more seasonal, like in the mountain forests of West Cameroon and in northeastern Tanzania, the reproduction of birds and small rodents predominantly occurs during the dry season (Serle 1981; Makundi et al. 2006).

On the other hand, the large species that had higher energy needs and that were big consumers of fruits were more dependent on this latter food, whether in terms of quantity or quality (Dubost and Feer 1992; this study). This was particularly obvious in white-lipped peccaries of Costa Rica where most births occurred from June to August when fruit availability was at its maximum (Altricher et al. 2001). These conditions greatly contrast with those present in the Kibale Forest (Uganda) where the lack of seasonality in fruit production of most tree species and in births of primates and rodents can be linked to the absence of a real dry season (Struhsaker 1997).

Contrary to what was predicted, there was no relationship between the seasonal percentage of reproductive males, beginning of gestation, or pregnant females and diet, except for seeds and leaves in the three largest species. This lack of a relationship was also true for the litters. This could be due to the small seasonal variations in diets. Nevertheless, the more important the role of fruits (pulp + seeds) was in the diet of the species, the more seasonal the litters were, as was the fruit production on the ground. Inversely, when species consumed a lot of animal matter, they gave birth more regularly during the year. On this point, *M. acouchy* was clearly distinguished from the other species by its greater consumption of fruits (particularly pulp), its lower diet diversity, and its halt in births over several months, as is the case for other mammals of similar size (Butynski 1988; Goldizen et al. 1988). A reason for such a difference could be that the *acouchy* almost exclusively inhabits forest areas, whereas the five other species also frequent more open areas

where the food variety is greater (Emmons and Feer 1990; Nowak 1999).

CONCLUSIONS

Contrary to the reproductive state of males, beginning of gestation and proportion of pregnant females, the percentage of litters appeared to be synchronous between the species and in phase with both the rainfall and fruit production in the field, regardless of the body mass, metabolic needs and gestation period of the species. This indicates that environmental factors at the time of birth are more important for the reproduction of these tropical species than proximal or median ones (at the time of fertilisation or during gestation). This corresponds well to what usually occurs in mammals of many other regions, where most litters are produced during the season most favourable for raising young, probably because of increased energy needs for mothers during the intense lactating period just after birth (Goldizen et al. 1988; Van Schaik et al. 1993; Bumrungsri et al. 2007). This implies that selection favoured the females who gave birth in the most appropriate seasons. The decrease in litter percentages over several months signifies that French Guiana could be considered as a seasonal region, despite its high level of annual rainfall. This is due to the long and severe main dry season.

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