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RESEARCH ARTICLE

Body Mass in Wild Bearded Capuchins, (*Sapajus libidinosus*): Ontogeny and Sexual Dimorphism

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Body mass is fundamental for understanding growth, health, and aspects of life history but records of body mass are rarely available for wild primates. We documented the body mass of all individuals in a group of wild bearded capuchin monkeys (*Sapajus libidinosus*) at annual intervals for seven consecutive years. Sexual dimorphism in body mass was more pronounced than reported in the literature for adults in this genus: females in our sample were relatively light (average 2.1 kg), while males had average body mass (3.5 kg). Three other notable differences between males and females were evident. First, males grew more rapidly and for a longer period than females. We estimate that males attained full body mass at 9.8 years of age and females at 7.5 years. Second, males showed greater inter-individual variability than females in growth rates and adult mass. Third, males gained about 20% above their baseline body mass upon becoming alpha, and lost that amount when they lost that status, but body mass in females was unrelated to social status. We also report preliminary data on mass and age of natal males at dispersal and mass and age at first reproduction for one female. The pattern of sexual dimorphism in ontogeny and inter-individual variability in body mass in bearded capuchins suggests different competitive risks in the two sexes commensurate with a mating system characterized by female choice of mates in multi-male, multi-female groups. Am. J. Primatol. 78:473–484, 2016. © 2015 Wiley Periodicals, Inc.

Key words: growth; emigration; mating system; life history; field methods

INTRODUCTION

Body mass is a fundamental biological variable, and a longitudinal record of body mass is a key index of growth and health. For these reasons, systematic longitudinal records of body mass are a standard component of animal husbandry and human health care. Equivalent records from individuals and populations in natural settings are sorely needed to understand health status of wild individuals, and therefore indirectly of a population, as well as for taxonomic comparisons and basic biological knowledge. These data allow us to understand, for example, how body mass relates to reproductive strategies and social status in animals [Leigh, 1995; Leigh & Blomquist, 2011; Pusey et al., 2005]. Growth rates can be related to brain size, metabolic rate, and behavioral ecology [Janson & van Schaik, 1993].

Leigh [1995], in an analysis of data from captive specimens of 37 taxa, documented two modes of dimorphic growth evident in sexually dimorphic species of nonhuman primates. Among species categorized as living in multimale–multifemale groups, males exceed females in body mass by maintaining a longer growth period than females, because males and females grow at an equivalent rate. Among species categorized as living in single male, multi-female groups, males exceed females in body mass by growing at a faster rate than females.

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However, Leigh [1995] noted considerable ambiguity in the data, and additional variables, such as differential risk of mortality between males and females and inter-male competition, also correlated with growth rates. O'Mara et al. [2012] describe a third pattern that is the combination of the two presented by Leigh [1995]: one sex grows faster and for a longer period (in the case of O'Mara and colleagues' study, female *Nycticebus* become larger than males through this third pattern).

In many primate species with multi-male groups, male social status is related to competition for reproductive females [Plavcan, 2011], and in some species social dominance among males is at least partly dependent upon contest competition. Competitive status is positively related to relative body mass in many species (e.g., golden hamsters and gray seals; Anderson & Fedak, 1985; Drickamer et al., 1973), and in primates, has been documented in mandrills (Dixson et al., 1993). Field researchers have noted that male white-faced capuchins (*Cebus capucinus*) appear to become larger following ascendance to alpha status and appear to become smaller following loss of alpha status ([Jack et al., 2014]; Susan Perry, personal communication). These observations are in line with variations in males' secondary sexual characteristics as a function of alpha status observed in mandrills [Setchell & Dixson, 2001a, b] and in male leaders of harems in hamadryas baboons [Kummer, 1971]. We do not know the magnitude of difference in mass between alpha males and other males in capuchins, however.

We have few data on the body of mass of wild primates [Johnson 2003], particularly from platyrrhines. Capuchin monkeys (genus *Cebus*, four species; genus *Sapajus*, the tufted capuchins, eight species) are medium-sized South American monkeys [Lynch-Alfaro et al., 2012a]. Wild-caught adults of the various species of capuchins weigh on average between 2 and 4 kg (average for all species, 2.3 kg, females, and 3.1 kg, males [Ford & Davis, 1992]; Fleagle [2013] gives slightly higher values). Note that the taxonomy of capuchins has been substantively revised in the past 15 years, which makes interpretation of the published literature about body mass in tufted capuchins problematic. Captive populations of tufted capuchins are all identified in the scientific literature until 2013 as *C. apella*, but in accord with the current taxonomy, they will be identified here as *Sapajus* spp., as recommended by Lynch-Alfaro et al. [2014]. Data on masses of individuals of all of the currently recognized species in the genus *Sapajus* will be useful for delineation of species characteristics.

Leigh's [1995] model leads to two alternative predictions with respect to the ontogeny of body mass in bearded capuchins: As they live in multimale–multifemale groups, male bearded capuchins should grow for a longer period than females, but at an equal rate. However, as reproductive success among males in capuchin groups is skewed toward the alpha male [Izar et al., 2009; Mendonça-Furtado et al., 2014; Muniz et al., 2010], making them in reproductive terms similar to single-male groups, males should grow at a faster rate than females. A third alternative is the pattern described by O'Mara et al. [2012], that males will grow at a faster rate and for longer than females.

Longitudinal data on mass gain in captive *Sapajus* spp. published prior to 2002 are summarized in Fragaszy et al. [2004]. Growth records from birth through 5.5 years are most extensive for *C. albifrons* from Fleagle & Samonds [1975] and Jungers & Fleagle [1980], and for birth through 8 years for *Sapajus* spp. from Fragaszy & Bard [1997] and Fragaszy & Adams-Curtis [1998]. Jungers & Fleagle [1980], who measured bone growth in young captive capuchins via radiographs taken weekly, biweekly, and later at intervals of 1–2 months from birth through 3 or 5.5 years, report continuous skeletal development through the first 5.5 years. Growth (measured as length of long bones) for the first 8 weeks after birth is nearly linear and rapid, and from 8 weeks through the first year slows considerably. The growth pattern described for capuchins by Jungers & Fleagle [1980] is characteristic of other primates, including humans. Longitudinal body mass data on one group of captive *Sapajus* spp. indicate that capuchins grow more slowly from 2 years (about 1.5 kg) until about 4 years (about 2 kg) than they do in the first 2 years [Fragaszy & Bard, 1997; Fragaszy & Adams-Curtis, 1998]. Thereafter, the growth curves for males and females appear to diverge, with females gradually increasing in body mass from 2 to 2.4 kg, and males increasing from 2 kg to 3.5 kg over the next several years (see also [Leigh, 1992]). Tufted capuchins in captivity have been noted to have a relatively large degree of sexual dimorphism (males weighing 1.9 times as much as females) that according to Leigh is mainly attributable to males growing for a longer time than females [Leigh, 1992]. Females in one group in captivity achieved their adult body mass at 5.5 years [Fragaszy & Adams-Curtis, 1998]. Average age at first conception was just after the 5th birthday (1,877 days), when females were 88% of their own adult mass.

Growth patterns relate to diet and foraging strategies and particularly to life history. Capuchins are recognized as possessing relatively extended periods of infancy and juvenility, large brains, and long life span [Fragaszy et al., 2004]. Brain tissue is metabolically expensive to grow and to maintain [Navarrete et al., 2011]. Janson & van Schaik [1993] suggest that the slow growth of juvenile capuchins reflects this taxon's strong reliance on extractive foraging strategies that require time to master for reasons of strength or skill (or both). These authors propose that slow growth through a lengthy juvenility reduces the likelihood of starvation for inefficient foragers. Ample data support the characterization of capuchins' (and especially tufted capuchins') diet as both tough [Wright et al., 2009] and requiring body mass and skill to process at adult rates of efficiency [Agostini & Visalberghi, 2005; Eadie, 2015; Fragaszy et al., 2010; Gunst et al., 2010; Melin et al., 2014]. At Fazenda Boa Vista, Brazil, observations of 17–19 month old bearded capuchins nursing daily from their mothers and allomothers (Michele P. Verderane, Dorothy M. Fragaszy, Elisabetta Visalberghi, Patricia Izar, unpublished data) indicate that weaning is an extended and gradual process among wild bearded capuchins, as among captive individuals [Weaver, 1999]. Although weaning is very gradual for capuchins, by 2 years of age they are responsible for feeding themselves, even if minimally equipped to do so in terms of body mass and skill. Nevertheless, young bearded capuchins eat the same foods as older members of their group [Chalk et al., 2015]. In captivity, female tufted capuchins reach adult mass by 6 years, and males at about 7 years [Fragaszy & Bard, 1997; Fragaszy & Adams-Curtis, 1998]. The length of time to achieve adult body mass is likely to be longer in natural settings than in captive settings (e.g., [Johnson, 2003]).

Groups of *Sapajus libidinosus* are typically cohesive, females are phylopatric and males disperse from natal groups [Izar et al., 2012]. Females compete aggressively (although mildly) for food and present a formal linear dominance hierarchy [Verderane et al., 2013]. All group members are integrated but subordinates are usually excluded from preferred food sources. Male–male relationships are characterized by despotic dominance hierarchy, male tenure can be 10 years or longer, and severe fights occur only during (rare) challenges to the dominant male [Mendonça-Furtado et al., 2014]. Immigrant males are gradually assimilated into the group with a progressive decrease in aggression and increase in tolerance. Reproductive success is highly skewed (>70% of observed matings) towards the dominant male due to female choice, as in white-faced capuchins [Izar et al., 2012; Mendonça-Furtado et al., 2014; Muniz et al., 2010]. The dominant male is the preferred affiliative partner of adult females, very tolerant to infants (as are all adults), and acts as a "policer" in group conflict management, *sensu* Flack et al. [2006].

Ecological models of social systems assume that socially dominant individuals have a competitive advantage in contest competition, and thus have better access to food than subordinate individuals [Janson, 2000]. The prediction drawn from these models is that mass should correlate modestly with social status among females. However, because females' reproductive success in the population of bearded capuchins at Fazenda Boa Vista does not appear to be limited by food availability [Izar et al., 2012; Verderane et al., 2013], we do not expect differences in mass among adult females.

We developed a simple, non-invasive method of weighing monkeys that enabled us to collect masses repeatedly from all members of a habituated wild group of bearded capuchins [Fragaszy et al., 2010]. Here, we describe the method and report the masses of individual wild bearded capuchin monkeys collected annually for seven consecutive years (2007–2013). We document growth for males and females from birth to 7 years, and provide masses for adults over consecutive years. We use these data to describe the overall pattern of mass gain and potential differences between males and females. These data allow us to test three hypotheses. Our first hypothesis is that social status correlates positively with body mass in males. Our second hypothesis is that the alpha male has the largest body mass among the adult males. Our third hypothesis is that females differ from males in that social status does not correlate with body mass in females as it does in males. We also report emigration and immigration. Although, we have a small N for these cases, we present the data here so that we may begin to accumulate data from wild populations of bearded capuchins for these variables.

METHODS

The experimental protocol was approved by the animal research committee (IACUC) at the University of Georgia and adhered to the Brazilian legal requirements, and to the American Society of Primatologists' principles for the ethical treatment of primates.

Site

We conducted the study at Fazenda Boa Vista (privately owned land) in Piauí, Brazil (9°39″S, 45° 25″W). Fazenda Boa Vista is an ecotone between Cerrado (open woodland) and Caatinga (semi-arid) biomes [Oliveira & Marquis, 2002] at approximately 420 m above sea level. This region has low-nutrient sandy soils and highly seasonal and inter-annually variable precipitation, between 800 and 1600 mm per year, the vast majority coming in the months of November–April [Oliveira & Marquis, 2002]. Despite strong inter-annual variability in precipitation, productivity of fruits and seeds in the region of the study group's home range was consistent across and within years from 2006 to 2008 [Verderane et al., 2013]. The monkeys' masses were measured in the outdoor laboratory area of our study site, which the monkeys visit regularly.

Subjects

All members of one group of bearded capuchins (*Sapajus libidinosus)* were weighed annually from 2007 to 2013. The group contained 20 to 24 animals (Table I); typically the group contained three adult males, six adult females, and 12–16 immatures. We have studied this group since 2005 and all members of the group are habituated to human observers at close range. The group was lightly provisioned with palm nuts and/or corn (average 234 kcal/monkey/day) during the period when we took these measurements (3–4 week period) in 2007 [Spagnoletti et al., 2012]. In subsequent years, we provided approximately the same amount of food but we did not measure it systematically.

One adult male in the group (Mansinho), was injured in June of 2010 and lost one foot in the next month. Another adult male (Jatobá), had four toes on one foot. One adult female (Amarelinha) suffered from an unknown progressive disorder that produced skeletal and joint deformities. She was non-reproductive despite exhibiting proceptive behavior and mating. All other individuals were intact and appeared normal, and no illnesses were noted during the period 2007–2013. Full records of births, immigration, disappearances, and change of alpha male status in the group were kept by the research team throughout the study period as part of normal demographic data collection.

Apparatus

We mounted an electronic scale (Cardinal Detecto 50 kg model, sensitivity to 10 g) on a tree using a metal stand (Fig. 1). The stand consisted of a vertical portion (73 high × 18 cm wide) that was strapped securely against a tree trunk. The horizontal platform (57 deep × 45 cm wide; 92 cm above the ground) on the stand was covered with gray/brown outdoor carpet and leveled after it was mounted on the tree. The scale was bolted to the stand and leveled. The stainless steel surface of the scale measured 36 cm deep × 46 cm wide. A removable stainless steel collar was attached to the distal portion of the platform; it supported a stainless steel bowl (25 cm diameter, 16 cm deep) with the rim 7 cm from the scale at its closest point. The rim of the bowl was the same height as the platform. We provisioned the bowl with water (approx. 2 liters) daily. The mass (to the nearest 10 g) of an object on the scale was displayed on a digital screen attached to the scale via a 280 cm long cable. An icon in the display signaled when the scale recorded a stable (reliable) value.

Procedure

The scale was readied and the bowl filled with water each day in advance of the monkeys' potential arrival in the outdoor laboratory area. We collected masses opportunistically as animals visited the water bowl over the course of a few hours on each day in which the monkeys visited the outdoor laboratory. The experimenter sat a few meters from the scale, viewing the digital display, and recorded the displayed mass when one animal paused or sat on the scale long enough to register a reliable mass. Infants' masses were taken in the same way, or calculated from masses taken of carrier and infant together, minus the carrier's (independently measured) mass.

Monkeys were weighed over a period of 2–3 weeks each year during mid-May to mid-June, except in 2010, when masses were taken in mid-August. We collected several masses for each individual and calculated its average mass to the nearest 100 g in each period. For purposes of calculating animals' ages at the date of weighing, the date of weighing was assigned as the middle of the weighing period.

Social status data were provided by Verderane [2010] and Mendonça-Furtado [2012] who studied social behavior in the same population during the periods when the mass data were collected in the first 4 years of this study (2007–2010). Rank was determined based on the direction of agonistic interactions recorded *ad libitum* during entire day group follows as part of other studies (e.g., Mendonça-Furtado et al., 2014; Verderane et al 2013). Yearly rates of agression between females and between males are reported in these studies. Considering the study period, we have analyzed 427 agonistic interactions involving females only and 388 interactions involving males only. Agonistic interactions were entered on an n × n matrix and analyzed using the Dominance Direct Tree, a method based on social network theory that decides dominance relationships based on the number of victories in conflicts, and resolves ties by transitiveness (Izar et al., 2006).

Comparisons of body mass in adult males and females were made using the Wilcoxon Mann Whitney test, with the two-tailed alpha threshold for significance set at a P value of less than 0.05.

RESULTS

Body Mass of Adults

Adults' masses across years are shown in Figure 2, and the full data set is presented in Table I. Overall, adults' masses remained stable across years. Adult males weighed substantively more than females (on average, 1.4 kg more) and there was no overlap in the masses of adult males and females (Wilcoxon–Mann–Whitney test, $n_1 = 5$, $n_2 = 7$, $U = 0$, $P \leq 0.01$). Subordinate adult males' masses varied from 3.4–3.6 kg (average = 3.5 kg; $N = 4$). Alpha males weighed 200–1000 g more

TABLE I. Body Mass (to Nearest 0.1 kg) and Ages (in Years and Days) at Date of Weighing of Wild Bearded Capuchin Monkeys (*Sapajus Libidinosus*) Taken Annually From 2007 Through 2013

				2007/6 July[a]			2008/1 June[a]			2009/ 5 June[a]		
Name	DOB[b]	Sex	Dam	Mass	Age[c]	Age[d]	Mass	Age[c]	Age[d]	Mass	Age[c]	Age[d]
Amarelinha	—	F	—	—	A	—	1.6	A	—	1.6	A	—
Chicao	—	M	—	4.4	A	—	4.2	A	—	—	A	—
Chiquinha	—	F	—	2.4	A	—	2.3	A	—	2.6	A	—
Chuchu	—	F	—	2.2	A	—	2.1	A	—	2.3	A	—
Dende	—	F	—	1.9	A	—	—	—	—	—	—	—
Dengoso	—	M	—	3.3	A	—	3.5	A	—	3.6	A	—
Dita	—	F	—	2	A	—	2.1	A	—	2.3	A	—
Jatobá	—	M	—	2.7	A	—	2.8	A	—	3.4	A	—
Mansinho	—	M	—	3.5	A	—	3.6	A	—	4.3	A	—
Piaçava	—	F	—	1.9	A	—	2.0	A	—	2.0	A	—
Teimoso	—	M	—	2.7	A	—	3.0	A	—	3.6	A	—
Teninha	—	F	—	2.2	A	—	2.1	A	—	2.0	A	—
Tucum	Jan 1 2005	M	Teninha	1.8	2.5	916	1.8	3.4	1247	2.4	4.4	1616
Caboclo	Jan 17 2005	M	Chiquinha	1.7	2.5	900	1.9	3.4	1231	2.2	4.4	1600
Pico	Nov 20 2005	M	Piaçava	1.2	1.6	593	—	—	—	—	—	—
Tomate	Dec 31 2006	M	Teninha	0.8	0.5	187	1.4	1.4	518	1.5	2.4	887
Catu	Feb 5 2007	M	Chuchu	0.6	0.4	150	1.3	1.3	482	1.5	2.3	851
Cangaceiro	Sept 20 2007	M	Chiquinha	—	—	—	—	—	—	1.5	1.7	624
Pati	Nov 2 2007	M	Piaçava	—	—	—	—	—	—	1.5	1.6	581
Doree	Nov 9 2007	F	Dita	—	—	—	—	—	—	—	—	—
Pamonha	Jan 2 2009	F	Piaçava	—	—	—	—	—	—	—	—	—
Paçoca	Jan 2 2009	F	Piaçava	—	—	—	—	—	—	—	—	—
Coco	July 14 2009	M	Chuchu	—	—	—	—	—	—	—	—	—
Chani	Feb 1 2011[e]	F	Chuchu	—	—	—	—	—	—	—	—	—
Thais	Feb 1 2011[e]	F	Teninha	—	—	—	—	—	—	—	—	—
Presente	Mar 15 2011[e]	M	Piaçava	—	—	—	—	—	—	—	—	—
Cachaça	Mar 15 2012[e]	M	Chuchu	—	—	—	—	—	—	—	—	—

		2010/ 8 August[a]			2011/31 May[a]			2012/ 28 May[a]			2013/ 24 May[a]		
Name	DOB[b]	Mass	Age[c]	Age[d]	Mass	Age[c]	Age[d]	Mass	Age[c]	Age[d]	Mass	Age[c]	Age[d]
Amarelinha	—	1.5	A	—	1.6	A	—	1.7	A	—	1.7	A	—
Chicao	—	—	A	—	—	A	—	—	A	—	—	A	—
Chiquinha	—	—	A	—	—	A	—	—	A	—	—	A	—
Chuchu	—	2.1	A	—	2.0	A	—	2.0	A	—	2.0	A	—
Dende	—	—	A	—	—	A	—	—	A	—	—	A	—
Dengoso	—	—	A	—	—	A	—	—	A	—	—	A	—
Dita	—	2.1	A	—	2.1	A	—	2.0	A	—	2.1	A	—
Jatobá	—	4.3	A	—	3.8	A	—	4.1	A	—	4.2	A	—
Mansinho	—	3.4	A	—	3.3	A	—	3.5	A	—	3.4	A	—
Piaçava	—	2.1	A	—	2.0	A	—	1.9	A	—	1.9	A	—
Teimoso	—	3.4	A	—	3.3	A	—	3.5	A	—	3.5	A	—
Teninha	—	2.0	A	—	2.2	A	—	2.0	A	—	2.1	A	—
Tucum	Jan 1 2005	2.9	5.6	2045	—	—	—	—	—	—	—	—	—
Caboclo	Jan 17 2005	2.8	5.6	2029	—	—	—	—	—	—	—	—	—
Pico	Nov 20 2005	—	—	—	—	—	—	—	—	—	—	—	—
Tomate	Dec 31 2006	1.7	3.6	1316	1.8	4.4	1612	2.0	5.4	1975	2.3	6.4	2336
Catu	Feb 5 2007	1.8	3.5	1280	1.8	4.3	1576	2.1	5.3	1939	2.5	6.3	2300
Cangaceiro	Sept 20 2007	1.7	2.9	1053	1.8	3.7	1349	2.1	4.7	1712	2.4	5.7	2073
Pati	Nov 2 2007	1.6	2.8	1010	1.7	3.6	1306	2.1	4.6	1669	2.5	5.6	2030
Doree	Nov 9 2007	1.3	2.7	1003	1.4	3.6	1299	1.6	4.6	1662	1.8	5.5	2023
Pamonha	Jan 2 2009	1.1	1.6	583	1.2	2.4	879	1.4	3.4	1242	1.6	4.4	1603
Paçoca	Jan 2 2009	1.0	1.6	583	1.2	2.4	879	1.3	3.4	1242	1.6	4.4	1603
Coco	July 14 2009	1.0	1.0	359	1.1	1.8	655	1.4	2.8	1018	1.7	3.8	1379
Chani	Feb 1 2011[e]	—	—	—	0.5	0.3	119	1.4	1.3	482	1.2	2.3	843
Thais	Feb 1 2011[e]	—	—	—	0.4	0.3	119	1.1	1.3	482	1.3	2.3	843
Presente	Mar 15 2011[e]	—	—	—	0.2	0.2	77	1.0	1.2	440	1.5	2.2	801
Cachaça	Mar 15 2012[e]	—	—	—	—	—	—	0.4	0.2	74	1.1	1.2	435

A, Adult.

[a] The day corresponding to the mid-point of the period in which body mass was collected that year.

[b] Date of birth.

[c] Age in years.

[d] Age in days.

[e] Estimated.

Fig. 1. Arrangement to obtain body mass of wild monkeys. A digital scale is mounted on the trunk of a tree in an area the monkeys visit regularly, and a bowl of water is placed at one end of the scale, so that a monkey visiting the water bowl passes over the scale platform. A digital display is placed a few meters away. A visual indicator appeared on the digital display when a stable mass was attained. We recorded an animal's mass only when it had four limbs on the scale platform and when the tail was not touching a surface other than the scale platform or was unsupported, and the monkey remained stationary long enough to register a stable mass value. Photo by S. T. Johnson.

than the other adult males in the group (3.8–4.4 kg, $N = 3$). The two males in our sample that attained alpha status during the study period gained between 700 and 800 g over their mass of the previous year (nearly one quarter of their previous mass), and one male (Mansinho) lost that same amount from the year in which he was alpha to the next year. Chicão, the largest male in our sample, was alpha in 2007 and 2008; he died in late 2008. For the years 2010–2013, when the same male (Jatobá) maintained alpha status and the social hierarchy among adults males remained stable, masses for all adult males in the group varied by 6% (sd for masses = 0.20 for an alpha male, 2010–2013; for two subordinate males in the same period, SD = 0.09).

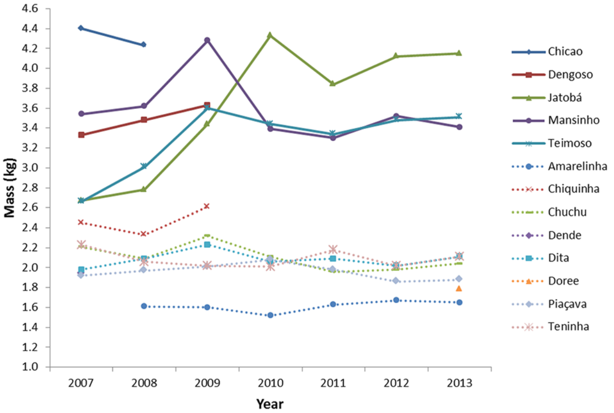

Fig. 2. Masses of the adult members of one group of bearded capuchins from 2007 to 2013. Dashed lines are females; solid lines are males.

Adult females weighed on average 2.1 kg ($N = 7$; range 1.8–2.6). We excluded from this calculation the anomalously small adult female with a progressive disorder (Amarelinha). Adult females' masses varied across years in relation to pregnancy. Females that were close to delivering an infant weighed up to 200 g more than when they were not pregnant (e.g., Chuchu in 2008, when not pregnant, weighed 2.1 kg and in 2009, 1 month before delivering an infant, she weighed 2.3 kg). The heaviest female, Chiquinha, disappeared in 2009 late in pregnancy, just after her mass (2.6 kg) was recorded. She was overtly healthy immediately prior to her disappearance. Doree, born November 9, 2007, delivered her first infant on Jan 16, 2013, at age 5 years and 65 days. Her infant survived to this writing (April 2015). Doree weighed the least of all reproductive adult females in 2013 (1.8 kg) following the birth of her infant, but she had gained 0.2 kg above her 2012 mass (1.6 kg).

Five adult females contributed masses in all years of the study. Two females disappeared (after providing masses in 2007 and 2009, respectively) and one female was categorized as adult in 2013 after she delivered an infant. Among the cohort of females that contributed masses in all years, social status was stable across years and it was not associated with individual differences in body mass. The alpha female in the study group across all years (Piaçava) weighed on average 2.0 kg, and the other three adult females averaged 2.1 kg (excluding from this calculation the anomalously small female Amarelinha). We calculated the standard deviation across years for the five adult females for which we have masses in all years. The standard deviation for each female was 0.08 kg.

Body Mass of Immatures

We have masses for 18 natal immature monkeys (8 M, 10 F; Table I). Of the individuals born in 2005, one (Pico) is assumed to have died at about 2 years of age, shortly after we obtained his body mass, and two (Tucum, Caboclo) to have emigrated. All others in the sample remained for the duration of the study. Our sample does not include two other live-born infants because they died before they were weighed. Two males, Tomate and Catu, born in late 2006 and early 2007, respectively, provided masses in all 7 years of the sample.

Figure 3 presents mass values for natal immature monkeys of each sex (data pooled across individuals within sex), and lines of best fit calculated with multiple regression. Note that female Doree's masses are provided through 2013 in Figure 3, to provide visual continuity for this individual, although she is classed as an adult in

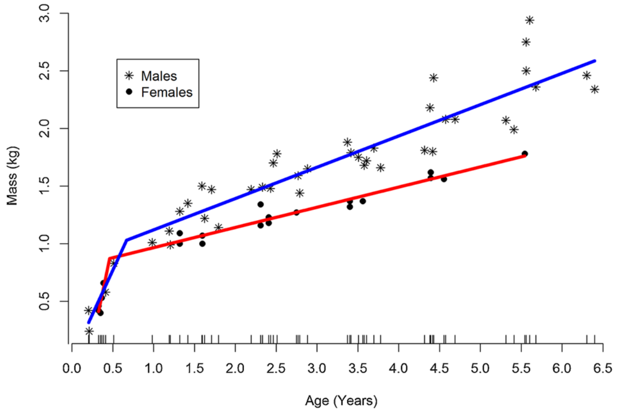

Fig. 3. Individual masses for male (stars) and female (circles) bearded capuchin monkeys through the first six years of life (N= 18). Lines of best fit were calculated using piece-wise linear regression in R. The inflection point between postnatal mass gain and later mass gain falls at 244 days for males (N = 4 masses prior to breakpoint) and 169 days, females (N = 5 masses prior to breakpoint). Adjusted $R^2 = +0.89$, males, and +0.98, females.

the 2013 sample (given that she had delivered an infant), and her 2013 mass appears also in Figure 2. Infants grew from < 500 grams in the first 100 days to 1 kg (50% of the mother's mass) or more after 400 days (1.1 years). There is no discernible difference between males and females in growth in the first year (but note that we have only four data points for males in that period, and five data points for females). Thereafter, females grew at a slower rate than males. Females would reach average adult mass (2.1 kg) in their eighth year (7.5 years) and males their average adult mass (3.5 kg) in their tenth year (9.8 years) if juvenile rates of growth were maintained unchanged.

Figure 4 displays individual growth trajectories for the seven immature males that contributed three or more successive annual masses to the data set. Individuals show greater consistency in growth rate (all adjusted R^2 values for individuals were +0.85 or higher) than seen across individuals (adjusted $R^2 = +0.79$ for all males, data pooled). In comparison, females showed strong similarity in growth ($R^2 = +0.98$ for all females pooled).

Emigration and Immigration

Two natal males (Tucum and Caboclo) weighed just less than 3 kg (2.9 and 2.8 kg) in 2010, a few months before they disappeared (and presumably emigrated) at just under 6 years of age. Two other natal males, Pati and Cangaceiro, weighed 2.5 and 2.4 kg, respectively, in 2013. A few months later, they disappeared (and presumably emigrated) a few months before their 6th birthdays. Four males immigrated into our study group in 2007 (Mansinho, Dengoso, Jatobá, Teimoso), just after the annual weighing period. All of them emigrated from the same neighboring group which was also habituated and under study by our team [Spagnoletti, 2009; Verderane, 2010]. In the weeks following the arrival of these immigrant males in the group, records show no reports of fights or wounding among males. The two heavier males (Mansinho, Dengoso) weighed 3.3–3.5 kg in 2007, 1 year after arriving in the group, and their mass increased just by 0.1–0.2 kg over the next 2 years (2008 and 2009). The two smallest of the four males (Teimoso and Jatobá) at their first weighing in 2007, about 1 year after their arrival in the group, weighed about 2.7 kg; these males gained about 0.8 kg over the next two years (2008 and 2009) to reach about 3.5 kg, the average adult male mass. Accordingly, we estimate that the two lighter males entered the study group when between 6 and 7 years of age, and the two heavier males when about 8–9 years old.

DISCUSSION

We provided body masses, measured annually over seven consecutive years, for all individuals belonging to one wild group of bearded capuchins. We focus our discussion on the lengthy duration of growth in bearded capuchins, the magnitude of sexual dimorphism in body mass in adult bearded capuchins in comparison to other species of capuchins, and on the ontogeny of dimorphism in body mass in bearded capuchins. The data allow us to test

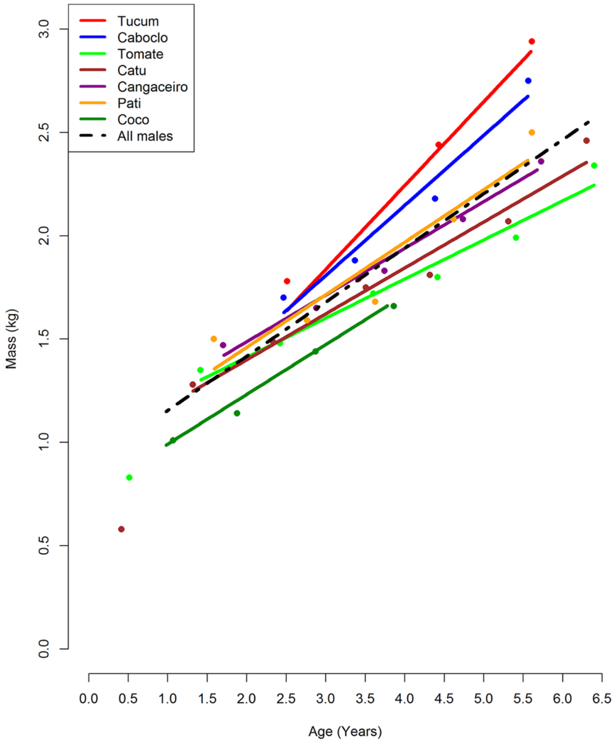

Fig. 4. Lines of best fit for mass gain by seven individual male bearded capuchins. Adjusted $R^2 > +0.85$ for each individual.

three hypotheses concerning the relation between social status and body mass in adults: (i) that social status correlates positively with body mass in males, (ii) that the alpha male has the largest body mass among the adult males, and (iii) that body mass in females does not correlate with social status as it does in males. We also discuss the implications of our data concerning age and body mass at immigration/emigration.

Sexual Dimorphism in Body Mass Among Species of Capuchins

Our findings indicate that adult female bearded capuchins at our study site weigh less on average (2.1 kg) than reported for wild female *Cebus capucinus*, *C. albifrons*, and *C. olivaceus*, that weigh 2.3–2.5 kg [Smith & Jungers, 1997]. Conversely, adult male bearded capuchins at our study site weigh more (3.5 kg), even when not alpha males, than wild *C. olivaceus* and *C. albifrons* (3.2–3.3 kg) and close to *C. capucinus* (3.6–3.7 kg) that were weighed without distinction by social status. Adult males in the current study are much heavier than wild adult male *Sapajus flavius* on average (2.8 kg), whereas female *S. flavius* have the same mass as female bearded capuchins in our sample (2.1 kg) [Montenegro, 2011]. There are no mass data available yet for other species of *Sapajus*, as the species in this genus were identified as separate species only in 2001 [Fragaszy et al., 2004], and the genus *Sapajus* was distinguished from *Cebus* more than a decade later [Lynch-Alfaro et al., 2012a, b]. Therefore, we can only compare our masses for *S. libidinosus* with those of capuchins belonging to the genus *Sapajus* without species distinction. According to Smith & Jungers [1997], who report masses for wild *C. apella* (pooling all species of *Sapajus* into one taxon), males weigh 3.6 kg and females 2.5 kg. Adult males in one captive colony of *Sapajus* spp. weighed 3.5 kg on average; females, 2.4 kg [Fragaszy & Bard, 1997].

It appears that female bearded capuchins at our site are lighter than females of most other species of capuchins, while the males at our site are the same mass or probably heavier than males of other species of capuchins (because the previously reported masses of wild males were reported without knowledge of social status and therefore included an unknown ratio of alpha and subordinate males in the sample). We should interpret the differences in body mass between males and females in the context of overall body conformation and behavioral ecology. The bearded capuchins appear to differ from the normative *Sapajus* body type in skeletal proportions that can be related to degree of terrestriality (higher in *S. libidinosus* than in others species of the genus [Wright et al., 2014]). For example, Verderane [2010] reports that *S. libidinosus* individuals at Boa Vista spend more than 30% of their active time on the ground [Verderane, 2010]. In Atlantic Forest, the congener *S. nigritus* spend less than 3% of their active time on the lowest vegetation stratum (0–4.9 meters; [Fogaça, 2009]). Despite substantive differences in the socioecology of *S. nigritus* and *S. libidinosus*, these two species share similar mating systems [Izar et al., 2012].

Ontogeny of Sexual Dimorphism in Body Mass

Jungers & Fleagle [1980] report that young captive capuchins (*C. albifrons and C. capucinu*s) of both species and both sexes exhibit most rapid skeletal development in the first 8 weeks, and continuous skeletal development through the first 5.5 years, when their study ended. Likewise, our data indicate more rapid growth in both sexes in the first year than later in bearded capuchins, and a steady rate of growth for both sexes from the second year through 6 years of age. Our method of measurement did not allow us to detect variations between the sexes at young ages, but it was sufficient to chronicle the differences between the sexes present in the second year and thereafter, and the range of variability within each sex. After the first year, females grow more slowly than males, and display little variation across individuals in body mass at any given age. Extrapolating from females' rate of gain, we can predict that females reach average adult mass (2.1 kg) in their eighth year, about 2 years later than reported for captive female *Sapajus* spp. [Fragaszy & Adams-Curtis, 1998]. The one female for which we have a mass record from her own birth to the birth of her first infant weighed 74% of the average adult female body mass two months before she conceived. She gained mass over the next year. This pattern is similar to that seen in mangabeys, mandrills, and macaques. Females of all of these species typically deliver their first offspring at 4–5 years, and achieve full adult body mass in their seventh year. Baboons, in contrast, postpone reproduction until they are more than 6 years old [Leigh & Bernstein, 2012], when they reach 89% of their adult body weight. Leigh and Bernstein suggest that a life history pattern of first reproduction well in advance of completion of somatic growth, as evident in mangabeys, mandrills and macaques, implies that females do not face a trade-off between somatic growth and reproduction.

Males show a more rapid growth pattern than females after the first year in our data, suggesting an organizational effect of prenatal and/or early postnatal androgenic hormones on growth (as in rhesus monkeys, *Macaca mulatta* [Abbott et al., 2009; Goy & Robinson, 1982; Kemnitz et al., 1988]. Fleagle & Samonds [1975] reported that male and female captive white faced capuchins, *C. capucinus*, followed different trajectories of mass gain beginning much earlier in life. Extrapolating from the male's rate of mass gain, we can predict that male bearded capuchins reach full adult mass (3.5 kg) in their tenth year. This estimate is in accord with field reports that male white-faced capuchins (*C. capucinus*) first attain alpha status when they are 10 years of age or older [Jack et al., 2014] although male *C. capucinus* as young as 7.8 years are known to have sired offspring [Muniz et al., 2010], and in captivity, much younger male *Sapajus* spp. have sired offspring [Fragaszy & Adams-Curtis, 1998]. Males show greater inter-individual variability in growth trajectories than do females, which may impact age at immigration, as we discuss below.

The ontogeny of sexual dimorphism that we find in our data seems intermediate to what Leigh [1995] proposes as two alternative modes of males becoming larger than females. As characteristic of multimale–multifemale groups, male bearded capuchin monkeys grow for 2 years longer than females (10 years, vs. 8 years). In addition, as characteristic of single male–multifemale groups, and as documented for *C. capucinus* by Fleagle & Samonds [1975] males grow more rapidly than females. Thus, they show both modes of generating sexual dimorphism in body mass, matching the pattern found by O'Mara et al. [2012] for *Nyticebus*. Comparisons with other species of *Sapajus* and *Cebus* may reveal if either or both of these two modes are stronger in *S. libidinosus* in comparison to congeners, that in general display less dimorphism.

Relationship Between Social Status and Body Mass

Another interesting finding is the marked increase in mass experienced by two adult male bearded capuchins upon gaining alpha status, and the loss by one male of an equivalent magnitude following loss of alpha status. In all years the alpha male weighed at least 0.5 kg more than the next heaviest adult male in the group (range 0.5–0.9 kg more; mean = 0.7 kg, 20% more), and was visibly bulkier, especially in the forequarters and head, than the other adult males. The pattern of obvious mass gain and loss that we observed in male bearded capuchins upon gaining or losing alpha status is similar to the reversible change in male secondary sexual adornments seen in mandrills upon reaching (or losing) alpha status in the group [Maggioncalda et al., 1999, 2000, 2002; Setchell et al., 2008, 2010]. The changes in mass experienced by males in our study group after gaining or losing alpha status are associated with rises or decreases in testosterone, respectively, as reported by Mendonça-Furtado et al. [2014] for this same group during the study period, and for *C. capucinus* observed under the same circumstances [Jack et al., 2014]. In short, our findings support the hypotheses that social status correlates positively with body mass in male bearded capuchins, and that the alpha male has the largest body mass among the adult males.

The relationship between social status and body mass is quite different for female bearded capuchins than for males. Whereas dominant male bearded capuchins weigh about 20% more than subordinate adult males, the dominant female is the same mass as other adult females in the group. Our findings support the hypothesis that body mass in females does not correlate with social status as it does in males. These results are in sharp contrast with those obtained by Pusey et al. [2005] for chimpanzees in which males' body mass is not associated with dominance whereas females' body mass significantly increases with dominance. The highest-ranking female chimpanzees were approximately 11% heavier than the lowest-ranking females. Also, within each sex, masses varied more among female chimpanzees than among male chimpanzees [Pusey et al., 2005].

Pusey et al. [2005] also report that social status correlated with temporal stability of body mass in wild chimpanzees. That is, more dominant individuals of both sexes maintained more stable body mass. Again, we found the opposite pattern in bearded capuchins: among female capuchins, we observed equivalent stability in body mass across years, regardless of social status. The same holds true for subordinate males. These species differences may reflect a different relationship between the social system and the overall health and reproductive success of individuals in the two species, sex bias in dispersal (male dispersal in capuchins, female dispersal in chimpanzees), different regimens of sexual competition, and/or different effects of food competition among females [Izar, 2004; Izar et al., 2009]. Alternatively, the consistent abundance of food in Boa Vista across the year and across years [Izar et al., 2012] may completely buffer individual variability in access to food across individuals. One might also propose that the slight provisioning of food to the study group during the few weeks per year, in which we collected mass data contributed to the stability in masses we observed across years. However, we did not find increasing mass within or across individuals across the period in which masses were collected in any year.

Age and Body Mass at Immigration

Four males emigrated from the study group at just under 6 years of age. All four weighed between 2.4 and 2.9 kg a few months before they left the group. Two other natal males, when about 8.5 years old and weighing 2.5 and 2.7 kg (in May 2014), had not emigrated. The two smallest of the four males that immigrated into the study group in 2007 weighed about 2.7 kg about a year later, and they gained about 0.8 kg over the next two years to about 3.5 kg, the average adult male mass. Their growth upon arrival in the study group was as rapid as that of immature natal males over the same period. Placing these males into the growth data for natal males, the lighter immigrant males were likely about 6 years old when they immigrated into the group. Taken as a whole, our data indicate substantial variability among males in age at emigration from their natal groups, but suggest that males are not likely to emigrate before they reach 2.4 kg.

In primates species in which males are heavier than females and males emigrate but females do not, emigrating males achieve full adult mass only some years after they leave their natal groups [Dixson, 2012]. Capuchin monkeys (both *Sapajus* and *Cebus*) fit this pattern [Jack et al., 2014; this study]. Dixson [2012] suggests that this pattern may allow young males to immigrate into a new group while they are lighter, and thus before they present a challenge to the resident alpha male. We observed both lighter and heavier males immigrate into our study group with relatively low aggression directed towards them or by them towards the resident alpha male until the ultimate contest for alpha status some years later. It would be interesting to document the immigration process in capuchin monkeys, with respect to aggression towards them by the resident males and females, and the reproductive careers of males that immigrate into a new group when they are relatively lighter versus relatively heavier, or that do not emigrate at all.

In conclusion, our findings fill an important gap in our knowledge of the biology of bearded capuchins. We hope that our non-invasive method of collecting body masses, or those developed by Cooper et al. [2004] and Mangalam & Singh [2013] can be adapted for use by other researchers studying arboreal monkeys, so that equivalent longitudinal information about other species in the genus and in other genera can be collected.

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