TITLE:

Demography and life history of a group of white-bellied spider monkeys (*Ateles belzebuth*) in western Amazonia

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SHORT TITLE:

Demography and life history of wild spider monkeys

ABSTRACT

Species-specific demographic parameters and life history variables are important for understanding how individual primate taxa have adapted to evolutionary and ecological pressures and for conducting interspecific comparisons as well as for conducting population viability analyses and for managing captive populations. Here, we describe results from a 12+ year study of the demographic dynamics of a wild group of white-bellied spider monkeys (*Ateles belzebuth belzebuth*) living near the Tiputini Biodiversity Station in a largely pristine rainforest in western Amazonia. Across the study period, group size varied between 25 and 37 individuals, and there was a clearly female-biased sex ratio within all age classes. Females were the dispersing sex, as 19 females born into the group disappeared close to reaching adult body size and were presumed to have emigrated, while seven subadult or adult females joined the group during the study period. We estimated the age of dispersal for females at 5.9 ± SD 0.4 years (N = 13). Our study confirms that males are the philopatric sex, as all natal males have remained in the group and some have begun to reproduce, while no males have immigrated. Males began ranging independently from their mothers at ~4.5 years of age and began copulating with adult females by the age of ~5 years. Females had long inter-birth intervals (44.2 ± SD 7.8 months; range: 32 – 64 months, N = 21). Based on our data, female spider monkeys might have longer life spans than males, as only one out of six adult males but 9 out of 11 adult females present in the group in mid 2005 were still present in January 2018. The slow development and extended life histories of wild spider monkeys pose significant challenges for the ability of these primates to cope with habitat degradation and hunting throughout their geographical distribution. (300 words)

KEY WORDS:

Atelines, Dispersal, Long-term studies, Philopatry, Reproduction

INTRODUCTION

Life history variables (such as survival and mortality rates, fertility, age at first reproduction, interbirth intervals and lifespan) are important parameters for understanding the evolutionary pressures faced by particular primate species as well as for conducting interspecific comparisons (Sugiyama, 2004; Leigh & Blomquist, 2010; Clutton-Brock, 2012; van Schaik & Isler, 2012; Bronikowski et al., 2016). Estimates of these parameters are also necessary for understanding age-structured population dynamics (Strier, 2014; Bronikowski et al., 2016) and for conducting population viability analyses (Pierson et al., 2015) and are important to the design and implementation of effective captive management and reintroduction programs. As anthropogenic activity and disturbance pervasively increases in natural habitats (Achard et al., 2002), the study of life history variables of wild populations living in relatively undisturbed areas is important for establishing baseline data that allow us to better understand how these changes impact wild populations (Clutton-Brock & Janson, 2012; Estrada et al., 2017). However, because the collection of life history variables requires a long-term investment in individual-based monitoring of primate groups, there is still relatively limited knowledge of life history characteristics in many long-lived species (Kappeler & Pereira, 2003; Strier et al., 2010; Bronikowski et al., 2016).

In the neotropics, the atelid primates (howler monkeys: *Alouatta*; spider monkeys: *Ateles*; woolly monkeys: *Lagothrix*; and muriquis: *Brachyteles*) are among the largest and longest-lived taxa of extant mammals and are considered important indicators of ecosystem health (Stevenson, 2011). Field studies on all four genera of atelids have contributed significantly to our understanding of their ecology and social behavior (Campbell, 2008; Defler & Stevenson, 2014; Di Fiore, Link, & Campbell, 2010; Kowalewski, Garber, Cortés-Ortiz, Urbani, & Youlatos, 2015; Strier, 2014; Strier, Possamai, & Mendes, 2015), but only limited data are available on life history parameters and long-term demographic dynamics of wild atelids, and only for a handful of wild populations (*Alouatta*: Neville, 1976; Rudran & Fernandez-Duque, 2003; *Ateles*: Shimooka et al., 2008; *Lagothrix*: Nishimura, 1990, 2003; *Brachyteles*: Strier, 2014). Here, we report the results of a 12+ year study of the demographic dynamics of one wild group of white-bellied spider monkeys (*Ateles belzebuth belzebuth*) living in a largely pristine rainforest in western Amazonia.

Spider monkeys typically live in large multimale-multifemale groups of 15 to 56 individuals, where adult females generally outnumber adult males (Shimooka et al., 2008). Spider monkey societies, like those of chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), are characterized by extremely flexible grouping patterns and manifest a high degree of fission-fusion dynamics (Aureli et al., 2008). Spider monkey groups are highly territorial, and the home ranges of neighboring groups overlap minimally, if at all (Symington, 1988; Di Fiore and Link, unpublished data). Female spider monkeys are reported to disperse from their natal groups as they reach sexual maturity (Di Fiore, Link, & Campbell, 2010; Di Fiore, Link, Schmitt, & Spehar, 2009; Shimooka et al., 2008; Symington, 1988), while male spider monkeys remain in their natal groups. Thus, spider monkey societies are considered to be structured around a core of related, philopatric males (Di Fiore, Link, & Campbell, 2010; Di Fiore, Link, Schmitt, & Spehar, 2009).

As one of the largest platyrrhines, spider monkeys are expected to have “slow” life histories, including a late age at first reproduction, long interbirth intervals, and a long lifespan (Promislow & Harvey, 1990), and, even when body size is controlled for, spider monkeys seem to have even slower life histories than expected compared to other platyrrhines (Di Fiore, Link, & Campbell, 2010; Harvey, Read, & Promislow, 1989). Still, due to the logistical challenges of conducting long-term studies of individually-recognized animals, data on most reproductive and life history parameters of wild spider monkeys remain limited. In a major review, Shimooka, et al. (2008) summarized the available demographic and life history data from 17 groups of wild spider monkeys that had been studied for periods of between 5 and 72 months (average 25 ± SD 20 months) at 13 sites spanning the genus’ geographic range. Data from the various sites suggest interspecific differences in interbirth intervals (IBI) for females, with *A. belzebuth* having the longest IBI (43.7 ± SD 5.1 months) and *A. chamek* (34.5 ± SD 5.8 months) and *A. geoffroyi* (31.9 ± SD 3.0 months and 32.0 ± SD 6.0 months) the shortest IBIs. However, even given Shimooka, et al.’s (2008) thorough review, data on dispersal patterns, age at dispersal, age at which immatures begin to travel independently from their mothers (but see Vick et al., 2008), age at first reproduction, and longevity are still scarce for wild populations of *Ateles*. For example, although previous studies have concluded that dispersal is strongly female-biased (as females often disappear from their natal groups when they are subadults, prior to mating, and new females sometimes join groups where researchers can recognize group members individually), the average age at dispersal for female spider monkeys is still unknown (Shimooka, et al. 2008).

Here, we use a combination of observational and genetic data from a 12.5-year study conducted at the Tiputini Biodiversity Station, Ecuador – one of longest-running field studies of spider monkeys – to provide estimates of key life history variables for wild white-bellied spider monkeys. We present data on age-sex composition across the study period and on age at dispersal and IBI for females, age at first independent travel for individuals of both sexes, and age at first observed mating and first successful reproduction for males. Data for this study come from one primary research group that, over the past year, seems to have progressed far into a process of permanent fission in which the original group has split into two smaller daughter groups. Estimates for these kinds of demographic parameters from wild populations of spider monkeys are critical for population viability studies and for modeling sustainability and extinction risk for these large-bodied primates, which are often targets for subsistence hunting and are sensitive indicators of anthropogenic habitat disturbance.

METHODS

Study Site and Subjects

Research was conducted at the Tiputini Biodiversity Station (TBS) in eastern Ecuador (76°08" W, 0°38" S). The field site comprises over 600 ha of old-growth tropical rainforest adjacent to Yasuní National Park (982,000 ha) and is part of the Yasuní Biosphere Reserve

(Figure 1). Annual rainfall at the site averages over 3000 mm. Data on the behavior and genetics of one main study group (MQ-1) have been collected over an approximately 12.5-year period (June 2005 – January 2018). During this time, the group varied in size between 25 and 37 individual spider monkeys. At the onset of the study, the group included six adult males and 11 adult females. Throughout the study, all group members were habituated to the presence of researchers and could be individually recognized through unique facial and anogenital characteristics. For the analyses below, we include all demographic and life history data collected on MQ-1 individuals through January 2018, while noting that data from the past year pertain to a time when the group was in the process of dividing into two daughter groups with progressively less contact between certain subsets of group members.

[INSERT FIGURE 1 ABOUT HERE]

Data Collection

Intensive observations of the MQ-1 study group began in mid 2005 and are ongoing, with occasional discontinuities in data collection, the longest being from September 2005 to July 2006 and from September 2015 to June 2016. Since the onset of the study period, we have regularly conducted full and partial day focal animal follows and *ad libitum* behavioral sampling on all adult group members, with observers attempting to rotate behavioral sampling across individuals.

During follows, the behavior of the focal individual was recorded at set intervals, and the identities of all animals in association with a focal individual (i.e., the "subgroup composition") were recorded continuously. That is, after identifying the initial composition of the subgroup of monkeys to which a focal animal belongs, we kept a continuous record of all changes in subgroup size and composition. Subgroup "fusion" events were scored as soon as an individual not previously observed in the subgroup was detected, while subgroup "fission" events – defined as when an individual that was previously present in a subgroup was not observed for >60 min (excluding resting periods) – were assigned post-hoc. From this continuous record, we extracted subgroup compositions at 15-minute interval and used these records for demographic and association analyses.

Individuals recorded in at least one composition record collected during a given month were considered "present" in the group during that month. For periods of discontinuity in data collection, when observers were absent from the field, we scored any individual spider monkeys who were recorded as "present" in the month before and the month after the break as "present" throughout the break. Similarly, if an animal was not recorded as "present" in a given month based on subgroup composition record data, but was present the month before and the month after, we inferred it to have been present.

During focal follows we also collected fecal samples from known individuals for DNA extraction and multilocus genotyping, using methods described previously (Di Fiore, Link, Schmitt, & Spehar, 2009). These genotypes have been used to estimate pairwise relatedness among group members and to evaluate maternity and paternity of infants born in the group using maximum likelihood-based methods (Di Fiore and Link 2011, 2016, and in preparation).

Finally, we compiled the timing of key demographic events (births, disappearances, presumed dispersals) from our long-term data as follows:

First, for all infants, we assigned the month and year of birth as the month in which they were first directly observed being carried by a female, unless an infant's physical appearance, mobility, or location of carriage (i.e., off of the ventrum) suggested it had been born more than a month previously and the mother had not been seen traveling unencumbered in the previous month. These latter cases were rare, but are not unexpected given the large home range size and highly flexible association patterns of spider monkeys. For the few cases where we had to infer a prior birth month for an infant, we assigned a date of birth of 1, 2, or greater than 2 months prior to first observation, based on the infant's developmental stage. We also confirmed the month of birth for some infants born early on in the study through photographic records from camera traps that we used to monitor spider monkey visits to a mineral lick that the group visited frequently (on average ~1x per week from August 2006 to April 2009; see details in Galvis, Link, & Di Fiore, 2014). We considered these **birth date estimates** to be "good" if infants were assigned a birth month 0, 1, or 2 months prior to first being observed.

We then calculated **interbirth intervals** (IBI) as the number of months between the month of birth of an offspring to a given female and the month of birth of her subsequent offspring, provided that the first offspring survived and was still present in the group at the time of the birth of its sibling. We only included IBI estimations when the dates of birth of both offspring were considered “good”.

We calculated **age at dispersal** for natal females as the difference, in months, between the month that a female was last seen in the group and her date of birth. We calculated **age at first independent travel** for natal individuals as the difference, in months, between the first day an animal was recorded traveling in a subgroup without its mother present and its date of birth. The **age at first copulation** by natal males was calculated as the difference between the first date the male was observed mating and his date of birth (natal females were never observed to copulate). Finally, to determine **age at first successful reproduction** for natal males, we calculated the difference between the date of birth for the first infant for whom a natal male was assigned and the natal male’s date of birth.

This research complied with protocols approved by the Institutional Animal Care and Use Committee (IACUC) at University of Texas at Austin and the University Animal Welfare Committee (UAWC) at New York University, adhered to Ecuadorian legal requirements, and adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Primates.

RESULTS

Demographic Dynamics and Longevity

Overall, between June 2005 and January 2018, a total of 77 individuals have been part of the MQ-1 study group of white-bellied spider monkeys. Adult females outnumbered adult males in the group in all study years, with the female-to-male sex ratio varying between 1.4:1 and 2:1. The number of adult males in the group at any given time ranged between 3 and 9, and the number of adult females ranged from 10 to 13 (Figure 2). As of January 2018, one of the daughter groups into which MQ-1 seems to have split contained 3 adult males and 6 adult females, while the other contained 4 adult males and 7 adult females. Throughout the study, all but the recently-immigrated (and presumably nulliparous) adult females had either one or two offspring with them at all times. Thus, the size of the original MQ-1 group varied between 25 and 37 individuals across the study period (Figure 2), and the sizes of the two daughter groups, as of January 2018, are 15 and 17 individuals, respectively. As of January 2018, more than 12.5 years after the onset of monitoring, only 11 out of 28 members of the group were still present. These included eight of 11 initial resident adult females, one of six initial resident adult males, and two immature males who reached adulthood during the study. Although at this point of the study we cannot robustly estimate the lifespan of wild spider monkeys in this population, based on the age of the oldest offspring of adult females resident in the group in 2005 – and given that females have their first offspring when they are approximately eight years old (see results below) – eight of the adult females in the population as of January 2018 must be at least 24 years of age. Moreover, given that males reach adulthood and begin reproducing around age seven (see results below), three of these females are estimated to be over 27 years of age as they were determined to be the mothers of males that were already adults in 2005. As of January 2018, these three females are still reproductively active.

[INSERT FIGURE 2 ABOUT HERE]

Infant Mortality

During the period between June 2005 and January 2018, a total of 42 known infants were born, including 30 females and 11 males, yielding a female-biased sex ratio among neonates of 2.7:1. We were unable to determine the sex of one of the infants born early in the study (2005) prior to its disappearance. In total, seven out of these 42 known infants (17%) disappeared and are presumed to have died before reaching one year of age, and an additional juvenile male disappeared at ~26 months of age. The factors influencing mortality or disappearance of immatures were unclear. Two female infants disappeared at <1 month and sometime between 12 and 22 months of age, simultaneously with their mothers. Three infant males disappeared within their first few days of life, and, for at least one of them, there was circumstantial evidence of intragroup infanticide (Alvarez et al., 2015). Finally, we could not determine the causes of disappearance for the three remaining offspring.

As noted above, five adult males disappeared from the original group during the study period, and we presume that these individuals died (rather than emigrated) as we have observed no cases of male immigration into the group (but see Aureli, Di Fiore, Murillo-Chacon, Kawamura, & Schaffner, 2013). Three of these males disappeared during a period of time characterized by a high rate of intergroup encounters (Link, 2011) and might have been killed or injured during episodes of escalated aggression between neighboring groups. In fact, during this period (2007–2008) we observed at least two adult males (one from our main study group and one from a neighboring group) with large, open wounds immediately following intergroup encounters. Three adult females also disappeared during the 12.5-year study, including two whose infants disappeared with them at the same time. These individuals also presumably died as there is no evidence of secondary dispersal in wild spider monkeys (Shimooka et al., 2008), and we have never seen either fully adult females or females with a dependent offspring immigrate into a group.

Female Interbirth Intervals

We calculated 21 interbirth intervals (IBIs) for females (N=10) who gave birth to an infant after the survival of a previous infant to the birth of its younger sibling. IBIs were approximately 3.7 years (44.2 ± SD 7.8 months; range: 32 – 64 months, N = 21). All but one of the females that gave birth to more than one offspring had both female and male infants (Table 1).

[INSERT TABLE 1 ABOUT HERE]

Dispersal and Philopatry

We were able to estimate age at dispersal for 13 females born during the study period. Females dispersed, on average, at 5.9 ± SD 0.4 years (70.8 ± SD 5.2 months; range: 63 – 79 months, N = 13). We were unable to estimate precisely the age at dispersal of two additional females that disappeared from the original group in 2015-2016 due to a discontinuity in data collection, but these females must have been between 64 and 70 months and between 65 and 71 months of age, respectively, when they left. Four additional females who were subadults at the onset of the study were estimated to have dispersed at a similar age, after almost reaching adult body size. Most natal subadult females were not observed ranging independently of their mothers for any significant amount of time before disappearing from the group. In fact, 15 of these females were in a subgroup with their mothers the last time they were seen, and another three were seen ranging with their mothers less than or equal to one week before their last sighting in the group. One subadult female spent 4.5 months regularly ranging independently of her mother within the home range of MQ-1 prior to their dispersal, and a second subadult female, who was last seen in November 2017, spent at least 5 months occasionally ranging independently of her mother before her mother disappeared between January and May 2015.

To date, we have not been able to determine the presence of any of the 19 females that presumably have dispersed from our focal group in two of the three neighboring social groups MQ-2 and MQ-3, both of which are partially habituated and whose demography we have monitored at frequently visited mineral licks using camera traps (see Methods in

Galvis, Link, & Di Fiore, 2014). Additionally, we were unable to localize a radiocollared subadult female who disappeared from the study group in 2007 during multiple searches for her signal upriver and downriver from the site. Together, these observations suggest that females are likely to disperse into groups that are beyond the neighboring territories of their natal group. We have not witnessed any cases of natal subadult females involved in copulations or any kind of reproductive activity prior to their dispersal. Finally, seven subadult females immigrated either into our original study group (N=5) or into one of the daughter groups (N=2) between October 2008 and January 2018, and several additional females joined the original group transiently for periods of between one and a few months (Figure 2). Five of the seven immigrant females first gave birth to infants in the group 20, 22, 42, 42, and 47 months after their immigration, and the sixth and seventh have only been present since November 2017 and January 2018, respectively.

The timing of independent travel and first reproduction are important milestones for male spider monkeys. Within our sample, we had three males for whom we can estimate the age at independent travel, as we knew their birth date and the date of first observation of those males traveling in a subgroup not containing their mothers. All three males were between 4 and 5 years old (53 months, 55 months, 56 months) when they began to frequently range independently from their mothers. For these same three males, we were able to estimate the age when they were first observed copulating with adult females. Each was first seen copulating soon after reaching five years of age, at 62, 62, and 66 months, respectively. Finally, for two additional natal males, we were able to calculate age at first successful reproduction based on paternity analysis. These two males sired their first offspring at ~79 months of age.

DISCUSSION

Some of the most notable characteristics of primates are their extended periods of juvenile development and their generally “slow” life histories compared to most other mammals, and explaining these general aspects of primate developmental biology – as well as explaining variation in life history strategy within different primate lineages – has been a major challenge for comparative evolutionary biologists (Harvey, Read, & Promislow, 1989; Ross, 1991). Slow maturation and long life spans in primates are associated with the need for extended infant and juvenile stages, where a large amount of parental investment is thought to be required in order to reduce predation or mortality on extremely “costly” offspring. Other authors have suggested that differences in developmental rates and lifespans across primates are related to important environmental variables, such as habitat type (Ross, 1991) and/or environmental unpredictability (Richard et al., 2002).

Our results help confirm that, amongst primates, wild spider monkeys in natural conditions have particularly slow life histories that closely resemble those of muriquis (Strier, 2014) and are more similar to those of apes than those of other monkeys of similar body weight (Di Fiore et al., 2011). The spider monkey’s slow life history is reflected at many stages throughout the life course: [1] infants and juveniles spend long periods of time (4.5 to 6 years) in close association with their mothers prior to social independence, [2] adult females have long interbirth intervals of approximately 3 to 4 years, and [3] individual animals can have very long lifespans in the wild.

Additionally, although our sample size is small, our results suggest that males and females both reach sexual maturity at relatively late ages for their body size compared to both other anthropoids and other platyrrhines. For example, three natal males in our original study group first began mating at 5 to 5.5 years, but did not sire offspring until more than a year to a year and a half later. For females, we estimate that mean age at first reproduction is somewhat older. Because mean dispersal age is approximately six years – and because females only give birth to their first offspring between 1.5 and 3 years after immigrating into a new social group – most females will not give birth before 7.5 years of age. Previous studies have estimated that female spider monkeys reached sexual maturity at around 6.5 years of age (Eisenberg, 1973; Milton, 1981), with first infants being born when mothers are between 7 and 8 years old (Chapman & Chapman, 1990). Thus, our observations of females dispersing at ~6 years of age fits well within the time frame that females would be reaching adulthood and transferring into other social groups. Previous information on age at emigration for female spider monkeys comes from Manu National Park, where Symington (1988) estimated the age of three female *Ateles b. chamek* who disappeared to be 4 to 5 years. Vick (2008) found that female *Ateles geoffroyi* from Punta Laguna, Mexico dispersed from their natal groups slightly later, at an average age of ~5.6 ± 0.5 years (66.6 ± SD 5.7 months, range=59 to 76 months, N = 8 females). Data from our current study suggests the age at emigration for female spider monkeys in Ecuador is even later and more similar to estimates for *Lagothrix* (6.0 ± SD 0.4 years) and *Brachyteles* (6.1 ± SD 0.6 years) and much later than that for female howler monkeys, who disperse around 2 to 4 years of age (reviewed in Di Fiore et al., 2011).

The average interbirth interval of female spider monkeys at TBS (44.2 ± SD 7.8 months) is similar to some previously published estimates for other spider monkey populations (Shimooka et al., 2008), but quite a bit higher than the estimate of 34.5 months for *Ateles b. chamek* in Manu National Park, Péru (Symington, 1988) and the estimate of 36.6 months for *Ateles geoffroyi* in Punta Laguna, Mexico (Vick, 2008). Potential explanations for these differences in IBI amongst different populations of spider monkeys are not clear, but may include factors associated with sample size, and further research is needed to determine if episodes of spontaneous abortion (Campbell et al., 2001), male-directed infanticide (Gibson et al., 2008; Alvarez et al., 2015), or degree of seasonality at different field sites (Shimooka et al. 2008) might help explain the variation. In fact, average interbirth intervals for female spider monkeys at TBS are amongst the longest reported for living atelines. Howler monkeys have much shorter IBIs than other atelines, between 16 and 22 months. Female woolly monkeys have an average IBI of 36.7 months (reviewed in Di Fiore et al., 2011), and female muriquis at Reserva Particular Patrimonio Natural-Feliciano Miguel Abdala in the Atlantic forest of Brazil have an average IBI of 35.8 months (Strier, 2014), both quite a bit shorter than the average interval we found for TBS *Ateles*.

Based on our long-term study of spider monkeys at TBS, dispersal seems to be strongly biased towards females, as has been reported for other populations. We recorded 19 subadult females disappearing from their natal group at, on average, ~6 years of age, and we observed seven females immigrate into the group, and two transient females were each observed in the group for a handful of months. Also, our data suggests dispersal events usually occur once in a lifetime in female spider monkeys, as most of the adult females that have been residents in the group are currently present in one of the daughter groups. Shimooka et al. (2008) also report no evidence of secondary dispersal in wild spider monkeys. Together, these observational data support previous molecular findings that males in our original study group are closely related to each other (with the exception of one male), while average genetic relatedness between adult females is low (Di Fiore et al., 2009). Interestingly, based on genetic parentage data, we also know that two of the adult males in each of the current daughter groups have paternal half-siblings among the set of males in the other daughter group.

Within primates, non-cooperatively breeding species tend to have birth sex ratios skewed towards the dispersing sex, as predicted by the Local Resource Competition hypothesis (Silk & Brown 2008). Consistent with this pattern, a number of studies have reported female-biased sex ratios at birth in populations of wild spider monkeys (Symington 1988; Shimooka et al. 2008; this study), and this pattern persists in adulthood. Thus, most studies of wild spider monkey groups with individually recognized animals report strongly skewed adult sex ratios, where adult females outnumber adult males roughly 2:1 (Shimooka et al. 2008 and references therein).

Male maturation in spider monkeys is estimated by determining when males begin traveling with other animals in subgroups that do not contain their mother, most commonly with older males. Milton (1981) observed male *A. geoffroyi* moving independently from their mothers during their fourth and fifth years of age, and this is roughly the same age at which we found male *Ateles belzebuth belzebuth* began traveling independently from their mothers. At Punta Laguna, too, Vick (2008) found that, while *Ateles geoffroyi* offspring of both sexes were consistently seen with their mothers until they reached 42 months of age, males began ranging in different subgroups between the ages of 42 and 60 months while females tended to continue to associate with their mothers.

As noted above, five of the six adult males that were originally present in the group in 2005 have disappeared, and we presume that these individuals died as there is no evidence of male dispersal at TBS (but see Aureli, et al. 2013 for one case of collective male immigration in *Ateles geoffroyi* in Costa Rica). Although the causes of their disappearances are not clear, several of these males vanished during a period of frequent and intense intergroup conflict and aggression (Link, 2011). Given that male spider monkeys jointly participate in cooperative territorial defense, boundary patrols, and incursions into neighboring territories – and given that intergroup relations between spider monkeys are invariably hostile – we suspect that some of the adult males might have disappeared in relation to escalating aggression between rival groups of males (see Aureli et al., 2006).

Primatologists have long appreciated the fact that the expected behavior of individual monkeys can be strongly influenced by demographic conditions (Strier, 2014), as variation in group size impacts the degree of within group competition and varying operational sex ratios influence the nature of male-female social interactions. But we are also coming to realize that many other aspects of the behavioral biology of nonhuman primates can be very sensitive to demographic fluctuations. For example, it has been argued that lethal intragroup aggression in spider monkeys (where adult males jointly cooperate in directing lethal aggression towards a subadult male) might take place in situations where female-to-male sex ratios are low and competition for females within social groups is more intense (Campbell, 2006; Valero et al., 2006). Demographic context can also influence the outcomes of intergroup encounters, as has been reported in chimpanzees where imbalances in numbers of males predicts the likelihood of escalated aggression between parties from different groups (Watts & Mitani, 2001; Wilson et al. 2012). Long-term field studies of known individuals provide valuable and fascinating datasets for examining how social and demographic conditions influence many aspects of primate behavioral biology.

Finally, it is important to note that in the current global economic climate, where primate habitats are pervasively being transformed into agricultural landscapes (Estrada et al., 2017), taxa with slow life histories – like spider monkeys – are particularly susceptible to anthropogenic habitat modifications (e.g., deforestation and fragmentation) and to direct threats associated with increased contact with humans (e.g., hunting, anthroponotic disease transmission). Spider monkeys not only have very stringent ecological requirements due to their specialist frugivorous diets (Di Fiore et al., 2008) and their strong preference for undisturbed forests, but they also are often preferred targets for subsistence hunting (Franzen, 2006). Having evolved a long period of juvenile dependency, a late age at sexual maturity, and long interbirth intervals may preclude spider monkeys from having sufficient flexibility to cope with the rapid changes that are currently taking place in their natural habitats (Ramos-Fernandez & Wallace, 2008; Estrada et al., 2017). In fact, spider monkeys are some of the first neotropical vertebrates to go locally extinct in fragmented landscapes (Michalski & Peres, 2005), making it even more important for conservation managers to have access to accurate estimates of demographic parameters from wild populations for use in sustainability and extinction modeling.

ACKNOWLEDGEMENTS

We are grateful to the Ecuadorian government and the Ministerio de Ambiente for permission to work in the Yasuní region and to the Universidad San Francisco de Quito and the directors and staff of the Tiputini Biodiversity Station for facilitating our primatological research at the site for over a decade. A large number of extremely dedicated Proyecto Primates research assistants helped to collect the demographic and behavioral data summarized here, including Laura Abondano, Cristian Alvarado, Sara Álvarez, Ricardo Arango, Marcela Córdoba, Nelson Galvis, Miguel García, Nausica de Gibert, Alice

Giunchi, Laura Gómez, Mauricio Guerra, Erin Fleming, Ryan Manders, Leonardo Mendieta, Ana Palma, Mónica Ramírez, Sebastián Ramírez, and Clara Scarry. Special thanks are due to David and Consuelo Romo, Kelly Swing, Diego Mosquera, Gaby Vinueza, Tomi Sugahara, Majo Rendón and all of the station's "tigres" who have provided continuous logistical support and friendship to our research team in the field. This project was funded by NSF SES 0726133, BCS 1062540, and BCS 1638822; the Wenner-Gren, L.S.B. Leakey, and Harry Frank Guggenheim Foundations, and the National Geographic Society.

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TABLES

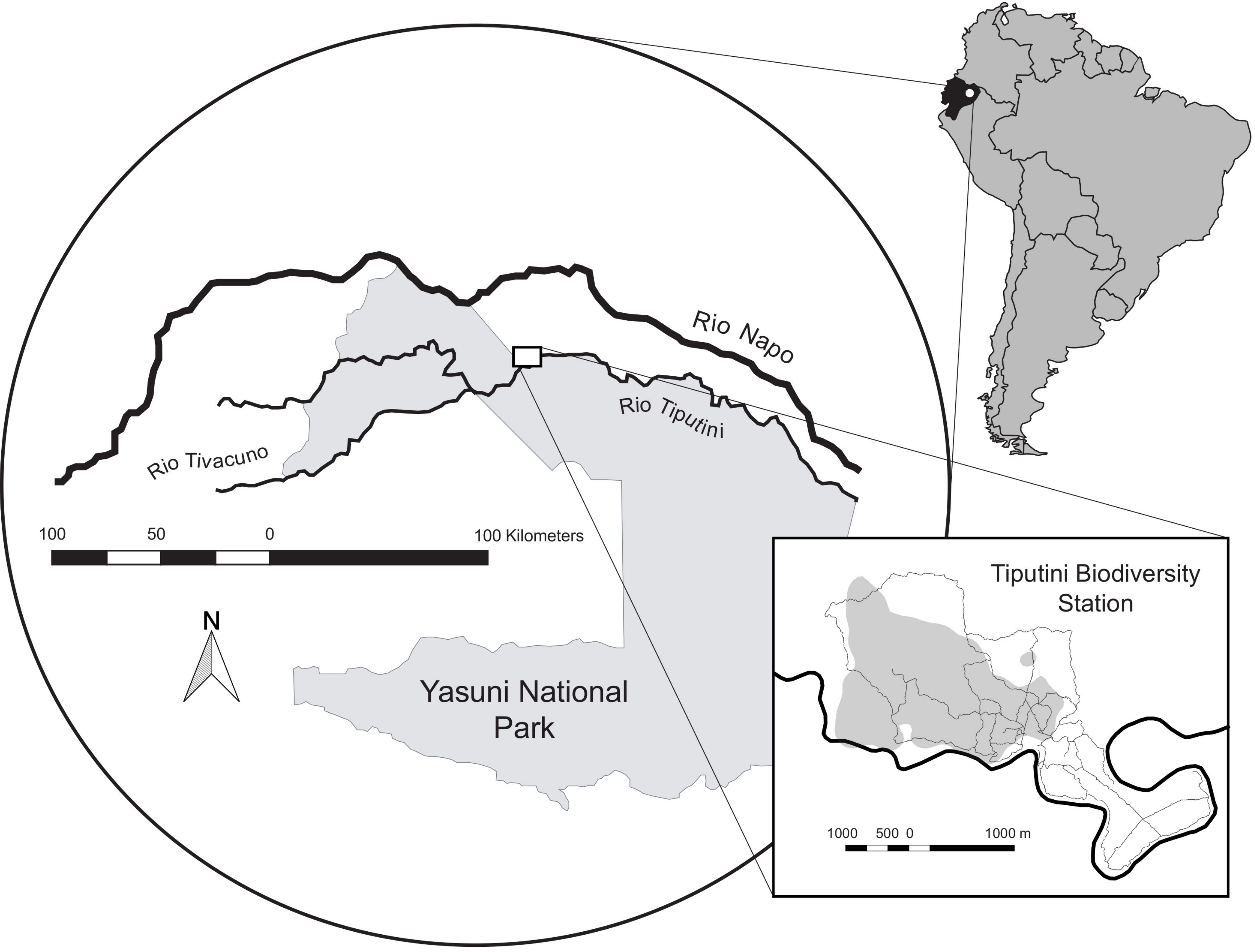
Table 1. Summary of offspring produced by each adult female over the course of the study. Five immigrant females who have given birth since immigration are indicated by asterisks (*), while three original residents indicated by crosses (†) disappeared during the course of the study.

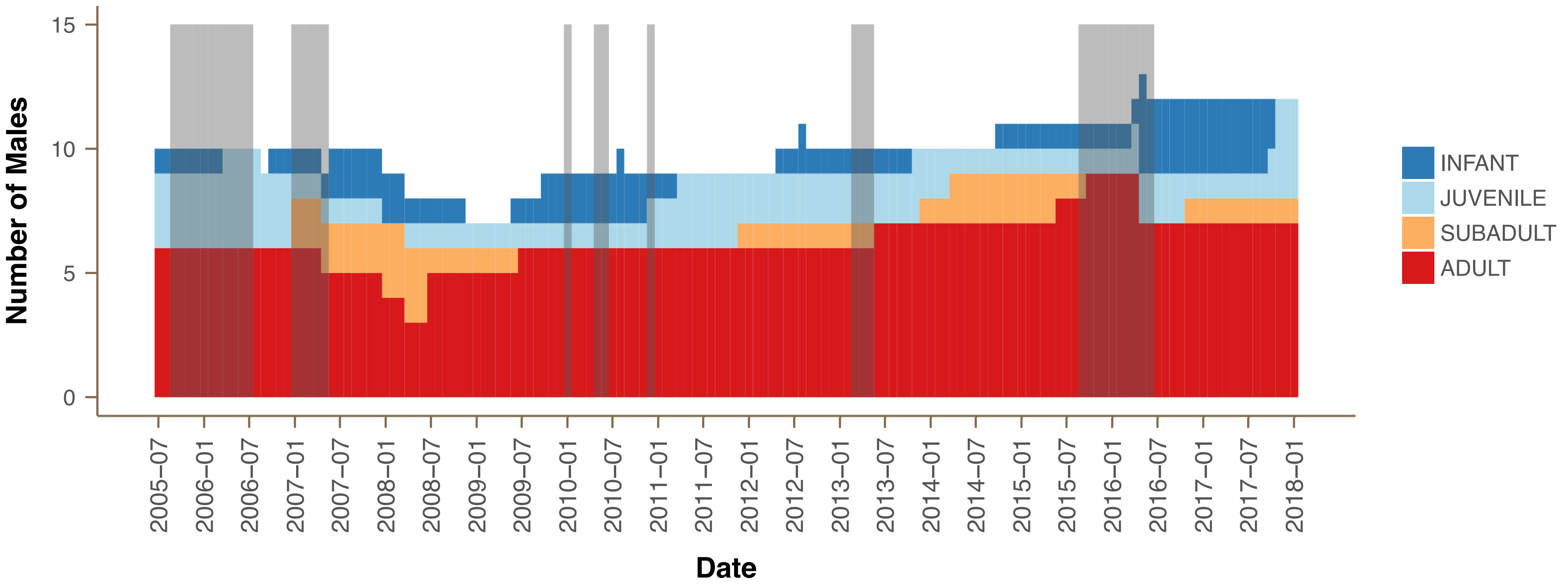
	OFFSPRING			
MOTHER	**MALES**	**FEMALES**	**UNKNOWN**	**TOTAL**
ANA	3	3	---	6
BUKA	1	2	---	3
COTINGA *	0	1	---	1
EVA	1	4	---	5
FIONA *	1	0	---	1
GISELLA †	1	1	---	2
JULIETA *	0	2	---	2
KAUO †	1	3	---	4
LUNA	1	4	---	5
MIKA	1	3	---	4
NIPA	1	3	---	4
OIKAMO †	1	1	1	3
RUMBA *	0	1	---	1
SOFIA	2	2	---	4
TAIGA *	0	1	---	1
VITA	1	2	---	3
TOTAL OFFSPRING	**15**	**33**	**1**	**49**
OFFPRING BORN SINCE 2005	**11**	**30**	**1**	**39**

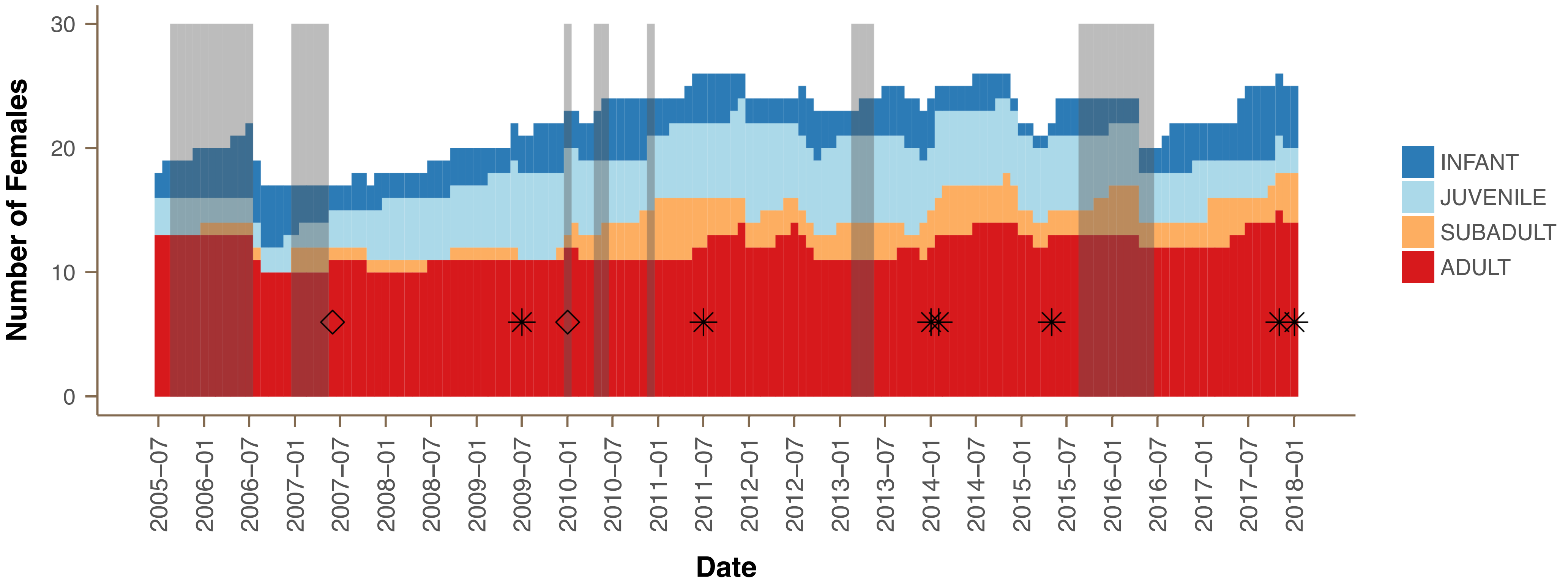
FIGURE LEGENDS

Figure 1. Location of the Tiputini Biodiversity Station within Ecuador and an overview of trail system at the study site. The 95% kernel density home range of the main *Ateles* study group, MQ-1, for the majority of the study is indicated with grey shading.

Figure 2. Summary of changes in the demographic composition of males (upper panel) and females (lower panel) in the main *Ateles* study group, MQ-1, since 2005. Periods of inconsistent observer presence are indicated by grey shading. Cases of immigrations (asterisks) and transient visitations (diamonds) by young adult females are also indicated in the lower panel.


Rio Napo
Rio Tiputini
Rio Tivacuno
100
50
0
100 Kilometers
N
Yasuni National Park
Tiputini Biodiversity Station
1000
500
0
1000 m


Number of Males
15
10
5
0
2005–07
2006–01
2006–07
2007–01
2007–07
2008–01
2008–07
2009–01
2009–07
2010–01
2010–07
2011–01
2011–07
2012–01
2012–07
2013–01
2013–07
2014–01
2014–07
2015–01
2015–07
2016–01
2016–07
2017–01
2017–07
2018–01
Date
INFANT
JUVENILE
SUBADULT
ADULT


Number of Females
30
20
10
0
2005–07
2006–01
2006–07
2007–01
2007–07
2008–01
2008–07
2009–01
2009–07
2010–01
2010–07
2011–01
2011–07
2012–01
2012–07
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2013–07
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2014–07
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2015–07
2016–01
2016–07
2017–01
2017–07
2018–01
Date
INFANT
JUVENILE
SUBADULT
ADULT