

## ARTICLES

DEMOGRAPHIC DYNAMICS OF PERUVIAN BLACK-FACED SPIDER MONKEYS (*ATELES CHAMEK*) REINTRODUCED IN THE PERUVIAN AMAZONFarah Carrasco-Rueda<sup>1</sup> and Raúl Bello<sup>2</sup><sup>1</sup>School of Natural Resources and Environment, 103 Black Hall, PO Box 116455, Gainesville, FL 32611, USA.

Email: &lt;farahcarrasco@gmail.com&gt;

<sup>2</sup>Kawsay Biological Station - Taricaya Ecological Reserve. Puerto Maldonado-Perú. Email: <perbello25@gmail.com>**Abstract**

Reintroductions of animals are important conservation tools for different taxa around the world. A reintroduction program in the Peruvian Amazon is focusing on black-faced spider monkeys (*Ateles chamek*). We investigated life-history parameters such as stage-specific survival and female fertility rates using a capture-mark-recapture framework and data from the literature. We estimated growth rate and probability of extinction for a reintroduced group using matrix models, as well as testing whether population growth depends more on survival of juvenile females or adult females. Our results suggest the population of the reintroduced group is decreasing. After projecting the group size for the next 25 years using different scenarios, we found that in order for the group to persist, survival rate of the female adult stage needs to exceed 79%. Given that group growth rate is more sensitive to the survival of adult females, management measures actions that target this demographic are required to guarantee survival of the group. Extrapolations of our results are subject to restrictions imposed by the small sample size and the conditions specific to this reintroduction program. However, this study may provide valuable lessons for reintroduction programs attempting the recovery of wild populations of similar species.

**Keywords:** *Ateles chamek*, Madre de Dios, matrix models, reintroduction**Resumen**

La reintroducción de animales es una herramienta importante para la conservación de diferentes taxa a lo largo del mundo. Un programa de reintroducción en la Amazonía peruana está enfocada en monos araña negros (*Ateles chamek*). Investigamos los parámetros de historia de vida tales como la tasa de supervivencia por etapa específica y fertilidad de las hembras, utilizando el marco de referencia de captura-marca-recaptura y datos de literatura. Estimamos la tasa de crecimiento poblacional y la probabilidad de extinción del grupo reintroducido utilizando modelos matriciales, asimismo, probamos si el crecimiento poblacional depende de la supervivencia en las etapas de hembras juveniles o adultas. Nuestros resultados sugieren que la población del grupo reintroducido está disminuyendo. Después de proyectar el tamaño grupal para los próximos 25 años utilizando diferentes escenarios, encontramos que para persistir la tasa de supervivencia de las hembras adultas debe exceder 79%. Dado que la tasa de crecimiento del grupo es más sensible a la supervivencia de las hembras adultas, las acciones de manejo deben enfocarse en este sector particular de la población para garantizar la supervivencia de la misma. Las extrapolaciones de nuestros resultados están sujetas a restricciones impuestas por el reducido tamaño muestral y las condiciones específicas del programa de reintroducción. Sin embargo, este estudio puede proveer lecciones valiosas para programas de reintroducción que intenten recuperar poblaciones silvestres de especies similares.

**Palabras clave:** *Ateles chamek*, Madre de Dios, modelos matriciales, reintroducción**Introduction**

Reintroductions consist of the re-establishment of species in areas of their historical range where they have become extinct or were extirpated (Seddon et al., 2014). Species from a variety of taxonomic groups have been successfully reintroduced in many parts of the world (barred bandicoot, Backhouse et al., 1994; bison, Pyne et al., 2010; black-footed ferret, Santymire et al., 2014; California condor, Walters et al., 2010; golden lion tamarin, Kierulff et al., 2012; gray

wolf, Bangs and Fritts, 1996; guanaco, Barri, 2016; red wolf, Hinton et al., 2013; scimitar-horned oryx, Woodfine and Gilbert, 2016; wild dog, Gusset et al., 2010). Reintroduction programs are considered a conservation tool (Kleiman, 1989; IUCN, 1998), a strategy to deal with defaunation (Barri, 2016), and a way to deal with individuals confiscated from illegal animal-trafficking operations (IUCN, 2002a). For species with high conservation value, the reintroduction process should be conducted under a well-defined management plan and result in reintroduced

individuals capable of survival in the wild without external intervention (Griffiths et al., 1989; IUCN, 2002b). Further, long-term post-release monitoring programs of reintroduced individuals or groups should be supported with knowledge about the species' ecology (Baker, 2002; Trayford and Farmer, 2012).

A number of non-human primate species have been reintroduced into the wild (Konstant and Mittermeier, 1982; Kleiman et al., 1986; King et al., 2011; Beck, 2017) with varying degrees of success. Black-handed spider monkeys (*Ateles geoffroyi*) on Barro Colorado Island (BCI), Panama, is an example of a successful reintroduction (Milton and Hopkins, 2005), which started with few individuals and currently has a healthy population.

Spider monkeys (*Ateles* spp.) are long-lived Neotropical primates that can live > 30 years (Link et al., 2018; Milton and Hopkins, 2005; Ramos-Fernández et al., 2017), and that exhibit long periods of maternal care (Di Fiore and Campbell, 2005). Male:female sex ratios in wild populations of *Ateles chamek* (aka *Ateles belzebuth chamek*) were reported in the range of 0.56-1 for adult and subadults (mean  $0.77 \pm 0.22$  SD, Shimooka et al., 2008). Spider monkeys have a high degree of fission-fusion dynamics (Aureli et al., 2008; Di Fiore and Campbell, 2005), where females disperse from social groups in search of new mates whereas males are philopatric (McFarland Symington, 1988). Unfortunately, most spider monkey species are considered as "Endangered", principally due to their long-lived, slow reproducing, and social nature makes them susceptible to habitat loss and overhunting (Mittermeier et al., 1989). The Taricaya Rescue Center started the "Program for the reintroduction of spider monkeys in the southeastern Peruvian Amazon" in 2009 with the goal of reintroducing rescued and rehabilitated black-faced spider monkeys (*Ateles chamek*) to the wild. The Peruvian government legally recognizes this program and approved of its management plan in 2012. Most of the spider monkeys in the program were seized from illegal traffickers or were being kept illegally as pets in Peru. Twenty two black-faced spider monkeys were released between 2011 and 2017 with the goal of establishing a stable, self-sustaining group. Since reintroduction, the program has carefully tracked the details of the release process and post-release monitoring activities, including monitoring animal behavior and resource use by the reintroduced spider monkeys (Bello et al., 2018). The future of the group, constituted by 13 individuals (10 females and three males) in 2017, is uncertain. Information on demographic dynamics and projections of population size over the next few decades is needed to help guide program management decisions and for planning future reintroductions.

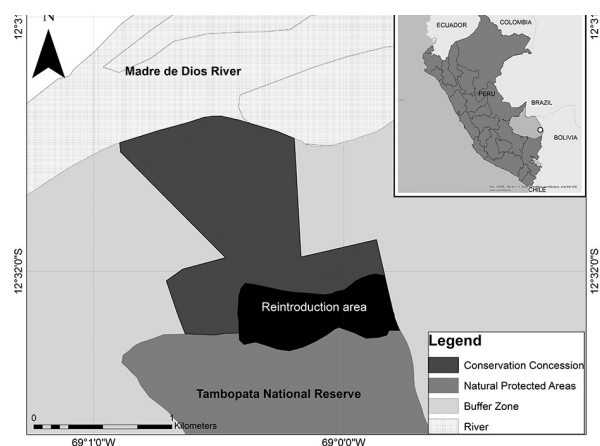
In this paper, we address the following questions: (1) What are the stage-specific survival rates and female fertility rates for the group of reintroduced black-faced spider monkeys?

(2) What is the group's population growth rate? and, (3) What is the probability of the group extinction in the upcoming decades? Based on what is expected for species that are slow to mature and have low reproductive rates (Stahl and Oli, 2006), we hypothesize that the population growth rate of the reintroduced group of black-faced spider monkeys is more sensitive to the survival of adults than to any of the other life stages. In this study we faced the challenge of working with the small sample size of only a single group of reintroduced black spider monkeys for estimating demographic parameters, which is why we also chose to include estimates found in the literature. The sample size limitation will restrict the extent to which context our results can be extrapolated, however, we consider this study to be important since reintroduction programs are only getting more common, but data available on reintroduced populations are scarce and the outcomes of these programs are not commonly reported.

## Methods

### Study Area

The reintroduction area is located on the south bank of the Madre de Dios River inside the Tambopata National Reserve in Madre de Dios Department, Tambopata Province, and Tambopata District in southeastern Perú ( $12^{\circ}32'11.882''$  S,  $69^{\circ}00'14.227''$  W, 601 m.a.s.l.) (Fig. 1). This area consists primarily of subtropical wet forest according to Holdridge life zones system; it may flood during the wet season (INRENA, 2003) and it experiences an average temperature and annual precipitation of 26.5 °C and 2,387 mm, respectively (SENAMHI, 2015). The dry season occurs from May to September and the wet season from October to April.



**Figure 1.** Map with the location of the reintroduction area in Madre de Dios, Perú.

### Spider Monkey Data

We utilized data from seven consecutive years (2011 to 2017) and four release events (2011, 2013, 2014, and 2016) of rehabilitated black-faced spider monkeys (*Ateles chamek*). Data were provided by the "Program for

the reintroduction of spider monkeys in the southeastern Peruvian Amazon". Data were collected by R. Bello and a team of volunteers during the post-release monitoring program. Individuals were identified by their body characteristics, face coloration and behavior, and were each assigned a name (Table S1 in Supplementary Material). During the first three months post-release, the activity of each individual was constantly monitored. Details about the monitoring procedure can be found in Bello (2018) and Bello et al. (2018). In the year following the post-release period, individuals were monitored during 2-3 days a week. Finally, following the first year after release, individuals were monitored twice a month to count individuals. Some individuals were equipped with radio tracking collars that allowed them to be located more easily. Individuals were considered dead if they were not sighted again after a month of searching. Each year that an individual was sighted again was considered a "recapture" in our analysis. Data collection on reintroduced black-faced spider monkeys followed international standard guidelines for non-human primate reintroductions (IUCN, 2002b).

Following MacFarland Symington (1988) and Shimooka et al. (2008), each individual was assigned to the following life stages: infants (0-12 months of life), juveniles (12-60 months of life), subadult (60-96 months), and adult (after 96 months or after the eight year of life). The data included in this study involved 28 individual life histories, 22 of them corresponding to individuals that were released into the wild when they were juveniles, sub-adult, or adults, and six of them that were subsequently born in the wild (Table S1 in Supplementary Material). Only six of the 22 reintroduced individuals survived in the wild to 2017. Predation by harpy eagles (*Harpia harpyja*; three events) and casual hunting (one event) accounted for the death of four reintroduced individuals. In seven cases (six females and one male) individuals disappeared and their current whereabouts remains unknown. Though they may have dispersed out of the study area, they were considered as deceased for the purpose of this analysis. In five cases, four of which were female, individuals in poor health conditions (individuals with fractures or infections) or individuals who separated from the group (Bello et al., 2018) were removed from the wild by the monitoring team and were taken to the Taricaya Rescue Center to recover. In some cases, a second reintroduction attempt took place once the individuals recovered to good condition. For the analysis, we did not consider data from individuals following a second attempt at reintroduction. Between 2013 and 2016, six individuals were born in the wild from reintroduced parents. In 2017, the group of reintroduced black-faced spider monkeys consisted of 12 individuals (1 adult male, five adult females, 2 young males, 4 young females), including six of the original reintroduced individuals and six new individuals that were born into this group post-reintroduction.

## Parameter Estimation

### *Capture-Mark-Recapture Model*

We used a Capture-Mark-Recapture (CMR) framework and Cormack-Jolly-Seber (CJS) models to estimate the survival parameters as used in other studies (Campbell and Lagueux, 2005; Cormack, 1964; Kraus et al., 2008; Olsen and Vøllestad, 2001). We estimated age-dependent survival-rate parameters for different life stages assuming post-breeding census. We assumed all individuals had the same probability of being detected, and that there was no migration into the group. To generate the models, we transformed observation histories for each individual into a Mark format database (Table S2, in Supplementary Material). Removal but not subsequent reintroduction of individuals were accounted for in the analysis, and we only considered individuals' life histories up until the first removal event. For analysis we pooled infants and juveniles into a single life stage "young" (infants correspond to young 1), as well as pooling adults and sub-adults for the analysis, since reproductive maturity has been reported to occur after the fifth year of life, especially in males (Klein, 1971; Eisenberg, 1976; Milton, 1981; van Roosmalen, 1985), but was also observed in females in this population (Bello et al., 2018; R. Bello personal communication).

We generated three models using data from 2011 until 2017, considering each year as a discrete occasion. The first model was based on age and sex; the second only using age of the individuals; and the third model was based on age from the female individuals only. Specific survival rates for females were used for further analyses related to fertility rate. We used program E-SURGE (Choquet et al., 2008; Choquet et al., 2011) to estimate probability of survival. Models were set to have the same probability of detection for all individuals and a recapture probability of one since all individuals were monitored. For details on how we defined the effects on the parameters for each model, see Supplementary material. We ran the models and selected the best model based on deviance values, quasi Akaike information criterion (QAIC) and QAIC corrected for small sample sizes (QAICc). The best model was used to estimate the following parameters: probability of an individual in young 1 stage to survive and grow to young 2 stage (P1); probability of young 2 stage to survive and grow to young 3 stage (P2); probability of young 3 stage to survive and grow to young 4 stage (P3); probability of young stage 4 to survive and grow to adult stage (P4); and the probability of individuals surviving and remaining as adults the next year (G5, Fig. 2). We considered P2 to P4 to be the same (see Supplementary Materials for model details). Due to the small sample size, we used a randomization procedure to generate simulated sets of samples. For this we draw one individual history at a time with replacement and extracted it from the pool of individuals of this study. With the randomly reduced pool of life-histories we ran the selected model in

E-SURGE using the package “R2SURGE” (Hines, 2017) in R (R Development Core Team, 2015) to estimate the survival probabilities. We repeated this 200 times to allow the model to approach the distribution of the estimated parameters. Next, we estimated the mean value of survival probability parameters and the confidence intervals for each of the different life stages. Additionally, we estimated the percentage of individuals per stage that survived along the study period, without considering the individuals that were removed from the wild.

#### Fertility rate

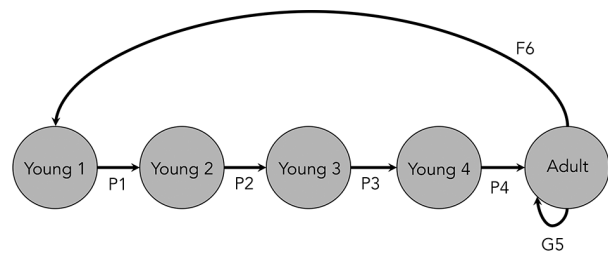
In order to estimate the fertility rate for females in the adult stage, we used an average inter-birth interval  $34.5 \pm 5.8$  months ( $2.88 \pm 0.48$  years) reported for *A. chamek* from wild populations in Manu National Park, Perú (McFarland Symington, 1988). In other words, on average 0.35 (range of values 0.3-0.42) individuals were born per year. Since spider monkeys rarely produce twins (Link et al., 2006), we standardized the number of offspring per birth to one. We considered the probability of newborns to be female as 0.73 (female:male sex ratio among neonates 2.67:1 for *A. chamek* in Symington, 1987; and 2.7:1 for *A. belzebuth* Link et al., 2018) so that the fecundity rate or average number of daughters per female spider monkey per year was 0.26 (range of values 0.22 - 0.31). Using data from our study site (2011-2017), we estimated fertility rates assuming post-breeding census calculated as  $l(i)/l(i-1)$ , where  $l(i)$  is the probability of surviving from birth to age  $i$  (Caswell, 2001). The estimated fertility rate for reintroduced individuals was pooled into the life stage “adults”.

#### Stage-Structured Matrix Models

We constructed a matrix model (Caswell, 2001) including survival rates per life stage (Fig. 2), including the fertility rate of adults (F6).

For estimating population growth rate ( $\lambda$ ) of the reintroduced group, we used the stage-specific survival-rate parameter estimates obtained with the CMR analysis. We projected the group size for the next 25 years - a period of time that covers the life cycle of an individual spider monkey. For our projection, we used nine individual females (number of females in the group by 2017) as initial group and different sets of values for the stage-specific survival parameters: (A) the estimated values, and (B) using parameter values reported in the literature for a wild population of *A. chamek* (survival probabilities young 1 = 0.67 and adults = 0.97; McFarland Symington, 1988) and *A. geoffroyi* (young = 0.9, from young to adult females = 0.9; Milton and Hopkins 2005).

We ran an elasticity analysis to determine which life-history parameters the population growth rate was more sensitive to, proportionally. With this information, we generated a fourth scenario (C) changing the parameter to which population growth was more sensitive by the threshold value at which the population would start growing if all other survival rate parameters had a value of one. For the analyses, we used the “popbio” package (Stubben and Milligan, 2007) in R (R Development Core Team, 2015).



**Figure 2.** Life cycle graph of reintroduced black-faced spider monkeys (*Ateles chamek*) in Madre de Dios, Perú, between 2011-2016. P1-P4 are the probability of survival from one state to the next. F6 is the fertility rate of adult individuals. G5 is the probability to remain in adult stage. Circles represent stage classes; arrows and arcs represent transitions in survival and fertility rates.

## Results

#### Parameter Estimation

Direct estimations using the data from individual histories showed that the percentage of individuals that survived the entire study period were: 100% for young in their first year of life (for both sex, 4 females and 2 males), 83% for females ( $n=6$ ) and 100% for males ( $n=1$ ) in young stage years 2 to 4, and 45% for adult females ( $n=11$ ) and 20% for adult males ( $n=5$ ).

Under the CMR framework the model based on data from only adult females showed the lowest QAIC value (Table 1). We used the survival rate parameters obtained from this model to estimate specific fertility rates for females and for further analysis (Table 2).

**Table 1.** Metrics of CMR models for *Ateles chamek*, Madre de Dios, Perú, data from years 2011 to 2017. QAIC<sub>c</sub> is QAIC corrected for small sample sizes.

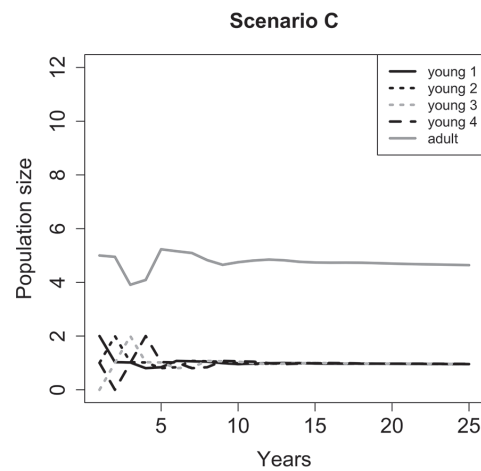
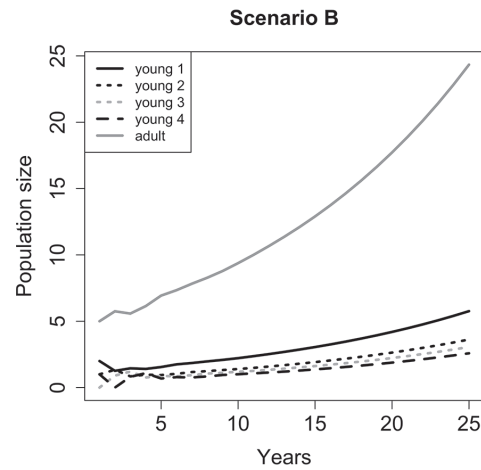
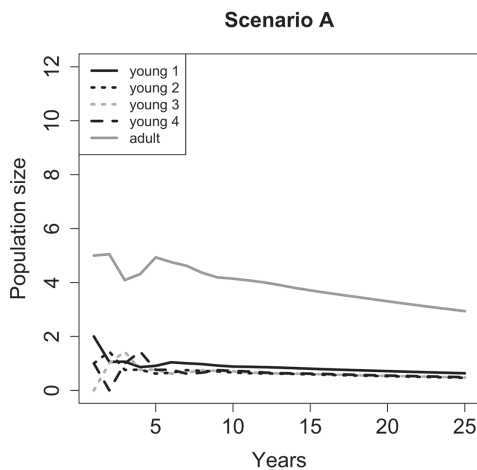
Model	Number of Parameters	Deviance	QAIC	QAIC <sub>c</sub>
Stage & Sex	7	51.99	65.99	67.54
Stage	4	53.55	61.55	62.09
Females	4	34.25	42.25	43.02

**Table 2.** Stage-specific survival and fertility rates for *Ateles chamek* in Madre de Dios, Perú, based on data from 2011 to 2017, for the following scenarios: (A) using estimated parameter values, (B) using parameter values reported in the literature (McFarland Symington, 1988; Milton and Hopkins, 2005), and (C) changing the parameter to which population growth is more sensitive to the value at which the population starts growing if all the other parameters are maximized. CI = Confidence interval.

Parameter	Stage	A	95% CI	B	C
Survival rate	Young 1	0.717	0.711-0.724	0.67	1
	Young 2	1	-	0.9	1
	Young 3	1	-	0.9	1
	Young 4	1	-	0.9	1
	Adult	0.81	0.809-0.813	0.967	0.79
Fertility rate	Adult	0.21	-	0.25	0.09

**Stage-Structured Matrix Models**

According to the group growth rates estimated using life history parameters for female individuals (scenario A), the reintroduced group will likely decrease ( $\lambda = 0.98$ ). Under scenario A, we expect that the group would decrease to only five individuals (Figure 3) over the next 25 years. Alternatively, scenario B ( $\lambda = 1.06$ ) predicts an increase in the population to 40 female individuals (24 adults and 16 young) by year 25. The elasticity analysis indicated that group growth rate was most sensitive to small proportional changes in the adult stage survival rate under scenarios A and B (elasticity values 0.49 and 0.67 respectively). When values of all other parameters are maximized (values of 1.0; scenario C), adult survival rate must be higher than 0.79 to achieve a positive group growth rate (Fig. 3).



**Figure 3.** Projections for a reintroduced group of *Ateles chamek* in Madre de Dios, Perú using data from 2011 to 2017 under scenarios with different sets of values of survival probability: (A) using the estimated parameter values, (B) using parameter values reported in the literature (McFarland Symington, 1988; Milton and Hopkins, 2005), (C) changing the parameter (to which group growth is more sensitive) to the value at which the group starts growing if all the other stage-specific parameters are maximized.

**Discussion**

Our results indicate that in order for this reintroduced group of black-faced spider monkeys to persist over time, it would be necessary to improve the probability of survival for female individuals, especially those in adult stages. The female-only model relies on the critical assumption that the group requires the presence of adult males to ensure its persistence in time, thus, the importance of males in the group cannot be disregarded. The reintroduced population of *Ateles geoffroyi* on Barro Colorado Island showed that the presence of one adult male might be enough to maintain the group (Milton and Hopkins, 2005). By 2017, our study group included one adult male, one infant male, and

one male juvenile of four years old. Losing the male individuals in the group will imply its extinction. The re-introduction program will need to guarantee the presence of males in the group over time to allow for breeding.

Under scenario A, and as a result of our small sampling size, the estimated survival probability for young 2, young 3 and young 4 was 1.0. The lowest estimated probability of survival was for female individuals in young 1 life stage. Probability of adult survival may be biased because we only had access to seven years of data, which is not enough to estimate real adult survival rates, considering adults of other species in the genus have been reported to live ~ 30 years (Milton and Hopkins, 2005; Ramos-Fernández et al., 2017). This should be taken into account when considering whether or not to utilize the estimated survival rates from this study in other contexts. The group remaining by 2017 was composed by 9 female individuals, accompanied by three males, which can be considered to be adapted to wild conditions. Group population growth rate based on estimates from our study group (scenario A) indicated that the reintroduced group was decreasing and would be close to extinction in 25 years. However, projections obtained under scenario B using parameters from the literature showed the potential for an increase in population size, reaching 40 individuals in 25 years. This last scenario is based on survival rate value for a combination of wild (*A. chamek*) and reintroduced (*A. geoffroyi*) individuals, which imply different conditions that may or may not be reached by the study group.

The elasticity analysis shows that the survival rate of adult females is critical for population growth. These results differ from those obtained in an elasticity analysis of a free-ranging *Ateles geoffroyi* population in Yucatán, Mexico, where survivorship of females during the first 5 years was critical (Ramos-Fernández et al., 2017; Ramos-Fernández et al., 2018). The same study also considered critical the fertility of females between 17 and 21 years old, which could not be measured in this study since we ignored the exact age of the oldest adult individuals in the group.

In the reintroduction experience at BCI, although only four individuals (3 females, 1 male) survived from a group of at least 18 individuals that were originally released, this was sufficient to allow the establishment of a group that persisted over the first seven years of the project (Milton and Hopkins, 2005). Even though the context and species considered are different from this study, it provides a good example of how resilient species in the genus *Ateles* can be. In this study, the group of monkeys reintroduced in Madre de Dios included five adult females of reproductive age and only an adult male of reproductive age since 2014, when a second male of reproductive age was killed in a hunting event. By December 2016, six new individuals had been born in the wild, including two offspring of the male killed in 2014. Since it is possible that

inbreeding problems will appear with only one reproductive male in the group, the survival of the other males until their reproductive maturity needs to be guaranteed. In order to secure the persistence of the population over time, female survival rate of adult females needs to remain above the specific thresholds of 0.79, below which the population size of the group will not increase.

There are several factors that were not considered in our analysis of group population growth and may have affected our results. First, under the CMR framework it is not possible to distinguish true mortality from permanent emigration (Hunter et al., 2010). This may be critical for spider monkeys because females emigrate to other groups. Indeed, apparently two of the reintroduced females, which are not in the group anymore, could have left after remaining in the group for only two and three years (R. Bello, personal communication). These individuals were in the age range for dispersal for *Ateles belzebuth belzebuth* (63 to 79 months, Link et al., 2018). Moreover, five female individuals were sighted two kilometers away from the study group in August 2017, in an area where the species is locally absent. According to Shimooka et al. (2008), females may travel long distances searching for new groups to join. It is likely that some of the individuals sighted away from the original group were considered as deceased in this study. Another factor not considered in our analysis is natal philopatry of males (McFarland Symington, 1988). While male immigration may occur under certain demographic circumstances (Aureli et al., 2013), this flexibility in their social system could influence the sex ratio in the group (Aureli et al., 2013). In addition, we do not include habitat measurements that would be useful to estimate the carrying capacity of the area where the reintroductions are taking place. Further, a study of the predator presence would be instrumental for management decisions, since they play a key role in the persistence of any group of spider monkeys (Shimooka et al., 2008).

Management actions are necessary to avoid extinction of the group of black-faced spider monkeys reintroduced to the Tambopata National Reserve in Perú. Specifically, actions should focus on minimizing mortality risk of adults and males in general. Reintroduced individuals that were previously kept as pets may have issues in their adaptation to the wild (Bello, 2018), despite the great efforts to prepare them made by the reintroduction program specialists. Reducing access of local hunters to the area, and temporary removal and subsequent release of injured individuals also might contribute to population growth. In addition, future attempts to increase the size of the group should focus on reintroducing reproductively fit individuals that arrive at the Taricaya Rescue Center in early life stages. Further, individuals that will be released together should spend their rehabilitation period as a group, avoiding future negative interactions in the wild. To have a self-sustaining population, establishment

of other groups of reintroduced individuals in the same area would be beneficial, as it would allow movement of females among groups. The final goal is to create a meta-population where the groups or populations could interact and persist over time.

Finally, extrapolations of our results to populations of free-ranging spider monkeys is not recommended due to the restrictions imposed to our results as a consequence of small sample size and specific conditions (i.e., intense post-monitoring program, reintroduction area without human activities). However, the life-history parameters we estimated may serve as reference for other reintroduction efforts. Most reintroduction programs start with only a few individuals sometimes releasing only one group that may not persist in the wild in the mid-term. However, this study may provide valuable lessons for reintroduction programs attempting the recovery of wild populations of similar species.

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## Supplementary material

### Model parameter definitions

We defined effects on the parameters for each model as follows. The first model is based on age and sex and we use

the notation  $g(3).a(1,2,3,4) + g(3).a(5) \& g(1) + g(4).a(1,2,3,4) + g(4).a(5) \& g(2)$ , In this model,  $g(3)$  correspond to young males,  $g(4)$  to young females,  $g(1)$  to adult males,  $g(2)$  to adult females, and “a” refers to the age of young individuals; the plus (+) sign separates individuals by stage and sex. In the section that corresponds to males,  $g(3).a(1,2,3,4) + g(3).a(5) \& g(1)$ , the first part (before the plus sign) accounts for the young males who stayed in that stage during the first four years of life. Since we deem the youngest individuals to have lower survival probabilities, we are considering the survival probabilities for ages 2, 3, 4 to be the same, the notation is  $(a(1,2,3,4))$ . The second part correspond to adult male individuals, including young males that reached the fifth year of life and became adults ( $g(3).a(5)$ ) as well as the ones that were adults when released into the wild ( $g(1)$ ). For female individuals, the interpretation is similar.

In the second model, the notation was  $g(1,2) \& g(3,4).a(5) + g(3,4).a(1,2,3,4)$ . The first part before the plus sign corresponds to the adult stages including individuals of both sexes that were already adults ( $g(1,2)$ ) and the young individuals from both sexes that became adults in their fifth year of life ( $g(3,4).a(5)$ ). The second part corresponds to young individuals of both sexes during each of their first 4 years of life:  $g(3,4).a(1,2,3,4)$ .

In the third model, we defined the effects on the parameters for the model as follows:  $g(1) \& g(2).a(5) + g(2).a(1,2,3,4)$ . The first part before the plus sign corresponds to the female adult stages that were already adults ( $g(1)$ ) and the young female individuals that became adults in their fifth year of life ( $g(2).a(5)$ ). The second part corresponds to young female individuals during each of their first 4 years of life:  $g(2).a(1,2,3,4)$ .

Table S1. Data for 28 individual life histories

ID	Sex	Age when released	2011	2012	2013	2014	2015	2016	2017	Comments
RIVER	female	adult	1	1	1	1	1	1	1	
ABIE	female	3	1	1	1	1	1	1	1	
MAQUI	female	adult	1	1	1	0	0	0	0	Removed
NIZZA	female	adult	0	0	1	0	0	0	0	Predated
WAWA	female	0	0	0	1	1	1	1	1	Born in the wild
LUCHA	female	adult	0	0	0	1	1	1	1	
MAYA	female	adult	0	0	0	1	1	0	0	Disappeared
CHOLA	female	adult	0	0	0	1	0	0	0	Disappeared
LILA	female	adult	0	0	0	1	1	1	1	
SHUSHU	female	adult	0	0	0	1	1	1	0	Disappeared

(cont.)

ID	Sex	Age when released	2011	2012	2013	2014	2015	2016	2017	Comments
CHINA	female	adult	0	0	0	1	1	1	1	
GAIA	female	0	0	0	0	0	1	1	1	Born in the wild
NICOL	female	adult	0	0	0	0	0	1	0	Disappeared
FE	female	adult	0	0	0	0	0	1	0	Disappeared
LOLA	female	0	0	0	0	0	0	1	1	Born in the wild
ALIAH	female	0	0	0	0	0	0	1	1	Born in the wild
NENA	female	4	0	0	0	0	0	1	0	Removed same year of release
FLACA	female	3	0	0	0	0	0	1	0	Disappeared
PACHA	female	4	0	0	0	0	0	1	0	Removed next year of release
MARUJA	female	5	0	0	0	0	0	1	0	Removed next year of release
SAMBO	male	3	1	1	1	1	1	1	1	
CHAMEK	male	4	1	1	1	1	0	0	0	Hunted
BALOU	male	3	1	0	0	0	0	0	0	Predated
SIMON	male	adult	0	0	1	0	0	0	0	Removed same year of release
OTTO	male	4	0	0	1	0	0	0	0	Predated
PERU	male	infant	0	0	1	1	1	1	1	
MARTIN	male	adult	0	0	0	0	0	1	0	Disappeared
RAYO	male	infant	0	0	0	0	0	1	1	

**Table S2.** Individual histories in Mark format for the 28 individuals considered in this study. First column shows the individual histories, second column correspond to adult males, third column to adult female, fourth column to young males and fifth column to young females. “-1” indicates the individual was removed from the group.

1111111	0	1	0	0;
1111111	0	0	0	1;
1110000	0	-1	0	0;
10000	0	1	0	0;
11111	0	0	0	1;
1111	0	1	0	0;
1100	0	1	0	0;
1000	0	0	0	1;
1111	0	1	0	0;
1110	0	1	0	0;
1111	0	1	0	0;
111	0	0	0	1;

10	0	1	0	0;
10	0	1	0	0;
11	0	0	0	1;
11	0	0	0	1;
10	0	0	0	-1;
10	0	0	0	1;
10	0	0	0	-1;
10	0	-1	0	0;
1111111	0	0	1	0;
1111000	0	0	1	0;
1000000	0	0	1	0;
10000	-1	0	0	0;
10000	0	0	1	0;
11111	0	0	1	0;
10	1	0	0	0;
11	0	0	1	0;