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Assessment of mammal reproduction for hunting sustainability through community-based sampling of species in the wild

Pedro Mayor,[1,2,3]* Hani El Bizri,[3,4] Richard E. Bodmer,[2,5] and Mark Bowler[6]

[1]Departament de Sanitat i Anatomia Animals, Universitat Autònoma de Barcelona, Bellaterra E-08193, Spain
[2]FUNDAMAZONIA, Malecón Tarapacá n° 332, Iquitos, Loreto, Perú
[3]Programa de Pós-Graduação em Saúde e Produção Animal na Amazônia, Universidade Federal Rural da Amazônia, Belém CEP 66077-901, Brazil
[4]Instituto de Desenvolvimento Sustentável Mamirauá, Tefé, Amazonas CEP 69553-225, Brazil
[5]Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Canterbury, Kent CT2 7NR, U.K.
[6]San Diego Zoo Global Institute for Conservation Research, Escondido, CA 92027-9614, U.S.A.

Abstract: *Wildlife subsistence hunting is a major source of protein for tropical rural populations and a prominent conservation issue. The intrinsic rate of natural increase. (*r_{max}*) of populations is a key reproductive parameter in the most used assessments of hunting sustainability. However, researchers face severe difficulties in obtaining reproductive data in the wild, so these assessments often rely on classic reproductive rates calculated mostly from studies of captive animals conducted 30 years ago. The result is a flaw in almost 50% of studies, which hampers management decision making. We conducted a 15-year study in the Amazon in which we used reproductive data from the genitalia of 950 hunted female mammals. Genitalia were collected by local hunters. We examined tissue from these samples to estimate birthrates for wild populations of the 10 most hunted mammals. We compared our estimates with classic measures and considered the utility of the use of* r_{max} *in sustainability assessments. For woolly monkey (*Lagothrix poeppigii*) and tapir (*Tapirus terrestris*), wild birthrates were similar to those from captive populations, whereas birthrates for other ungulates and lowland-paca (*Cuniculus paca*) were significantly lower than previous estimates. Conversely, for capuchin monkeys (*Sapajus macrocephalus*), agoutis (*Dasyprocta sp.*), and coatis (*Nasua nasua*), our calculated reproductive rates greatly exceeded often-used values. Researchers could keep applying classic measures compatible with our estimates, but for other species previous estimates of* r_{max} *may not be appropriate. We suggest that data from local studies be used to set hunting quotas. Our maximum rates of population growth in the wild correlated with body weight, which suggests that our method is consistent and reliable. Integration of this method into community-based wildlife management and the training of local hunters to record pregnancies in hunted animals could efficiently generate useful information of life histories of wild species and thus improve management of natural resources.*

Keywords: Amazon, community wildlife management, hunting sustainability, intrinsic rate of natural increase, production model, r_{max}

Evaluación de la Reproducción de Mamíferos para la Sustentabilidad de la Caza a través del Muestreo Comunitario de Especies en Vida Libre

Resumen: *La caza de subsistencia de fauna silvestre es una importante fuente de proteína para las poblaciones rurales tropicales y un tema prominente de conservación. La tasa intrínseca de incremento natural (*r_{max}*) de las poblaciones es un parámetro reproductivo clave en las evaluaciones de la sustentabilidad de*

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*email mayorpedro@hotmail.com

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la caza más utilizadas. Sin embargo, los investigadores se enfrentan a dificultades graves para obtener datos reproductivos en vida libre, así que estas evaluaciones generalmente dependen de tasas clásicas de reproducción calculadas en su mayoría a partir de estudios de animales cautivos y realizadas hace 30 años. El resultado son errores en casi el 50 % de los estudios, lo que obstaculiza la toma de decisiones sobre el manejo. Realizamos un estudio de 15 años en el Amazonas en el cual se utilizaron datos reproductivos de los genitales de 950 hembras de mamíferos cazados. Los genitales fueron recolectados por los cazadores locales. Examinamos el tejido de estas muestras para estimar las tasas de gestación de las poblaciones silvestres de los diez mamíferos más cazados. Comparamos nuestros estimados con las medidas clásicas y consideramos la utilidad del uso de $\mathrm{r}_{\mathrm{max}}$ *en las evaluaciones de sustentabilidad. Para el mono lanudo (*Lagothrix poeppigii*) y el tapir (*Tapirus terrestris*) las tasas de gestación en vida libre fueron similares a las de poblaciones cautivas, mientras que las tasas de nacimiento de otros ungulados y de la paca de tierras bajas (*Cuniculus paca*) fueron significativamente menores que los estimados previos. En el caso contrario, para los monos capuchinos (*Sapajus macrocephalus*), agutíes (*Dasyprocta sp.*) y coatíes (*Nasua nasua*), nuestras tasas reproductivas calculadas excedieron enormemente los valores frecuentemente utilizados. Los investigadores podrían seguir aplicando las medidas clásicas compatibles con nuestras estimaciones, pero para otras especies las estimaciones previas de* $\mathrm{r}_{\mathrm{max}}$ *pueden no ser apropiadas. Sugerimos que sean utilizados datos de estudios locales para establecer cuotas de caza. Nuestras tasas máximas de crecimiento poblacional en vida libre estuvieron correlacionadas con el peso corporal, lo que sugiere que nuestro método es consistente y confiable. La integración de este método al manejo comunitario de la fauna silvestre y al entrenamiento de los cazadores locales para registrar las gestaciones de los animales cazados podría generar eficientemente información útil sobre la historia de vida de las especies silvestres y así mejorar el manejo de los recursos naturales.*

Palabras Clave: Amazonas, manejo comunitario de fauna silvestre, modelo de producción, r_{max}, sustentabilidad de la caza, tasa intrínseca de incremento natural

Introduction

In tropical regions, wildlife subsistence hunting is a traditional source of food for rural human populations and of foremost importance in conservation (Miller-Gulland & Akçakaya 2001). A wide range of species is targeted, but many are mammals, which may be threatened by overhunting (Fa et al. 2002). Ensuring wildlife hunting is sustainable, secures long-term benefits for people, and conserves species and ecosystems. Species conservation and priorities are often guided by assessments of the vulnerability to extinction or sustainability of hunting of the target species in a given area (IUCN 2012*a*).

The ability of different preys to withstand various levels of harvest without depletion varies with the population dynamics of the species (Caughley 1977). Sustainability of harvests therefore hinges on methods for measuring the abundance of hunted wildlife populations (Mills 2012) and on estimating life-history parameters (Robinson & Redford 1986). One of the most used methods for assessing hunting sustainability is the production model (Robinson & Redford 1991), which has become a standard model in sustainability analyses (e.g., Alvard et al. 1997; Robinson & Bennett 2000; Ohl-Schacherer et al. 2007) and accounts for over 34% of all assessments (Weinbaum et al. 2013). A key parameter of the production model is a measure of the reproductive performance of target species, the intrinsic rate of natural increase (r_{max}), calculated using Cole's equation (1954): $1 = -e^{\mathrm{rmax}} + be^{-\mathrm{rmax}(a)} - be^{\mathrm{rmax}\ (w+1)}$, where a is the age at first reproduction, w is the age at last reproduction, and b is the annual birthrate of female offspring. For populations not limited by food, space, resource competition, or predation and parasites, r_{max} is the maximum possible increase in number (Caughley 1977; Robinson & Redford 1986). Therefore, r_{max} can be used to predict how particular prey species will respond to different levels of harvesting (Greene et al. 1998) and r_{max} is used in models to determine the sustainability of hunting, such as the production model with survival probabilities (Slade et al. 1998), source-sink models (Joshi & Gadgil 1991), and spatial models (Levi et al. 2011). The key value used to calculate r_{max} is the annual birthrate of female offspring, which is also used in a range of hunting models, such as the harvest model (Robinson & Bodmer 1999) and the unified harvest model (Bodmer 2004). Annual birthrate is also used in population viability analyses (Akçakaya & Sjögren-Gulve 2000) and calculations of minimum viable population size for several species, the results of which are used to determine International Union for Conservation of Nature threat status (IUCN 2012*b*).

The use of inaccurate reproductive estimates strongly influences calculations of sustainability, but researchers are often hampered by a lack of basic biological data (Miller-Gulland & Akçakaya 2001). For instance, wildlife managers using the production model or other algorithms that depend on r_{max} have been criticized for employing classic standard measures of reproductive performance provided by Robinson and Redford (1986), most of which were obtained from captive studies conducted at least 30 years ago. These standard values are thought to consistently inflate estimates of production and to exaggerate estimates of sustainable exploitation (Miller-Gulland & Akçakaya 2001). In a sensitivity analysis with 33 comparisons, the production model failed to detect unsustainability, whereas unsustainability was detected by other methods in 58% ($n = 19$) of the cases (Weinbaum et al. 2013). And the production model cannot be used to determine sustainable hunting because in any particular case, the maximum possible production may not have been reached (Robinson 2000).

Studying the life histories of long-lived mammal species by traditional means can take years and in tropical areas is beset by logistical and financial restrictions. Accordingly, few reproductive life histories have been estimated in the field (Duncan et al. 2007). Estimates for $r_{\max}$ are typically made with data from captive populations maintained under low-density, high-resource conditions (Caughley 1977). However, the maintenance of wild species in captivity may produce reproductive variations due to multiple factors, such as the stress of captivity, availability of resources, mates, territories, and the composition of social groups, all of which may differ substantially from wild conditions. Seasonal variations on food availability are often circumvented in captive populations and likely have strong impacts on reproduction (Goodman 1999; Mayor et al. 2011). Such variation suggests that reproductive estimates obtained from captive systems may be appropriate for estimating maximum reproductive parameters, but even wild populations not limited by food, space, and resource competition may not be able to achieve these estimates. Furthermore, data on captive reproduction are unavailable for many, often endangered, species mainly because they are not reproducing well in captivity (e.g., red uakari [*Cacajao calvus*] [Becker et al. 2013] and woolly monkey [*Lagothrix poeppigii*] [Bowler et al. 2014]).

Despite the severe limitations of reproductive parameters derived from captive data, they are frequently used in models that estimate the sustainability of hunting and subsequently influence conservation policy. We propose that estimates of the rate of increase in wild populations based on reproductive parameters determined from hunted populations living in relatively undisturbed areas with conserved natural resources will provide a better understanding of their reproductive life history and may be more appropriate for sustainability analyses.

We derived life-history parameters from the genitalia of hunted animals through collaborative methods with the local communities harvesting from the populations under analysis. Local communities depend on subsistence hunting for food and could become active samplers of valuable biological material that is usually discarded. We used biological samples collected over 15 years by community members to estimate wild reproductive rates of hunted mammal populations in the Peruvian Amazon. We compared estimates of annual birthrate of female offspring between field and captive populations and considered the use of $r_{\max}$ of wild mammal populations for use in sustainability studies and extinction modeling.

Methods

Study Area

The study area spanned 107,000 ha of continuous forest, predominantly terra firma, on the Yavari-Mirin River in the northeastern Peruvian Amazon. Within the study area, there was only 1 community, Nueva Esperanza (04° 19′ 53"S; 71° 57′ 33" W; UT-5:00), with 307 inhabitants. Members of the community hunt an area of 422 km^2 that is surrounded by a virtually unhunted area of around 1500 km^2. The climate is typically equatorial with an annual temperature of 22–36 C, a relative humidity of 80–100%, and an annual rainfall of 1500–3000 mm. The seasons are dry (May–October) and wet (November–April).

Sample Collection

From 2000 to 2015, as part of an ongoing participatory conservation program that involves local hunters in implementing community-based wildlife management, 13 subsistence hunters collected genitalia from hunted adult female animals, labeled them with a code, and preserved them in buffered 4% formaldehyde solution (v/v). From 2000 to 2008, local hunters collected only the internal and external genitalia, including ovaries, uterus, vagina, and vulva. From 2009 to 2015, the sample collection included all thoracic and abdominal organs, which allowed assessment of the health of individuals (Mayor et al. 2015). Samples were collected in all seasons, and hunters recorded the species, date, location, and individual code for each sample. Although all hunted species were collected, we analyzed only species with >20 samples (Table 1).

Reproductive Performance

We identified females as mature based on the presence of at least one embryo or fetus (pregnant) or of active corpora lutea or antral follicles in the ovaries (Mayor et al. 2013). For the latter, we examined slices of ovaries with standard histological methods to search for the presence of these structures. We recorded the number and sex of fetuses in each pregnancy. Because first anatomical signs of pregnancy are observed around the 15th day of gestation (Mayor et al. 2005), a possible underestimation of 10% of pregnancies was expected. Reproductive information is deposited in Pangaea (http://doi.pangaea.de/10.1594/PANGAEA.862140).

We calculated the average monthly and seasonal (dry and rainy seasons) pregnancy rates and the annual pregnancy rate. We used the seasonal pregnancy rate for species with seasonal sample collection, and the annual pregnancy rate for species with a nonseasonal sample collection. We also calculated litter size. We used pregnancy rate and litter size to calculate yearly reproduction

Table 1. **Monthly, seasonal, and annual pregnancy rates based on the examined genitalia for which there was a collection date.**

Order and scientific name[a]	*Sample size*	*Average monthly pregnancy rate*	*Average seasonal pregnancy rate*	*Pregnancy rate in dry season*	*Pregnancy rate in wet season*	*Annual pregnancy rate*	*Pregnancy length (days)*	*Reference (pregnancy length)*
Rodentia								
Cuniculus paca	212	0.673	0.628	0.576	0.68	0.656	149	Guimarães et al. 2008
Dasyprocta sp.[a]	43	0.691	0.661	0.621	0.7	0.665	104	Nieuwendijk 1980; Guimaraes 2000
Primates								
Lagothrix poeppigii	86	0.307	0.338	0.313	0.363	0.341	225	Mooney & Lee 1999 (*Lagothrix* sp.)
Sapajus macrocephalus[a]	30	0.281	0.31	0.312	0.308	0.233	153	Di Bitetti & Janson 2001 (*Cebus apella nigritus*)
Cacajao calvus[a]	21	0.258	0.354	0.28	0.427	0.357	153	Di Bitetti & Janson 2001 (*Cebus apella nigritus*)
Carnivora								
Nasua nasua[a]	56	0.2	0.222	0	0.444	0.286	75	Whiteside 2009
Artiodactyla								
Tayassu pecari	194	0.401	0.405	0.387	0.423	0.402	158	Roots 1966
Pecari tajacu	204	0.453	0.423	0.417	0.43	0.426	138	Mayor et al. 2005
Mazama americana[a]	83	0.437	0.449	0.46	0.438	0.447	210	Muller & Duarte 1992
Perissodactyla								
Tapirus terrestris[a]	21	0.575	0.725	0.85	0.6	0.743	385	Kasman et al. 1985

[a] *Species with smaller sample sizes than needed to produce a confidence limit of 10%.*

and annual birthrate of female offspring as follows: yearly reproduction = 365 days ∗ pregnancy rate ∗ litter size/gestation length, and annual birthrate of female offspring = yearly reproduction ∗ ratio of female fetuses. Gestation length was obtained from studies conducted in captive populations (Table 1).

We also calculated $r_{\max}$ as an estimate of the rate of population increase under the wild conditions at our study site and compared our $r_{\max}$ with Robinson and Redford's (1986) estimates of $r_{\max}$ derived from captive populations. Because populations at our site may be at levels where they are still resource limited, our values may be underestimates. However, where our values exceed those of Robinson and Redford's (1986), our value may be considered an alternative estimate of $r_{\max}$. We used a variation of Cole's (1954) equation to calculate our $r_{\max}$: $1 = \text{-e}^{r\text{max } i} + \text{be}^{r\text{max}\,(a)} - b\text{e}^{r\text{max}\,(w+1)}$. We used our estimates of the annual birthrate of female offspring for the parameter *b* and Robinson and Redford's (1986) values of *a* and *w*.

No animals were killed other than those harvested as part of local hunter's usual activities. The research protocol was approved by the Servicio Nacional Forestal y de Fauna Silvestre of Peru (Research Ethics Committee for Experimentation in Wildlife Protocols number 041-2007-DGGFS-DGEFFS; 0350-2012-DGFFS-DGEFFS).

Statistical Analyses

To test the seasonality of sample collection, we transformed each collection date into the degrees of a circle (1 January = 0.986° though to 31 December = 360°) and applied circular statistics with a Rayleigh's uniformity test performed in R version 2.15.1 (R Core Team 2012) and R package circular (Agostinelli & Lund 2011) to assess whether sample collection dates were randomly distributed throughout the year (following Carnegie et al. 2011). Differences with a probability of 0.05 or lower were considered significant.

We used the EpiInfo7 (Epi info, Center for Disease Control, Atlanta, Georgia, U.S.A.) package to calculate the minimum sample size for a population survey conducted with simple random sampling. Data were expected pregnancy rates (obtained from our results), and we applied a 5–10% confidence limit, a 95% confidence level, and assumed an unlimited population size.

Following Hennemann (1983), we used Pearson correlations to test the relationship between the log of the body weights of species and their intrinsic growth rates calculated by us and by Robinson and Redford (1986). Primates were excluded from these analyses because primates usually exhibit lower $r_{\max}$ than would be predicted for their body mass due to their differential metabolic rates (Hennemann 1983). Adult body weights were obtained from Robinson and Redford (1986).

Results

From 2000 to 2015, hunters registered 246.4 preys per year on average (46.2% females and 53.8% males). The most frequently hunted mammals were *Tayassu pecari* (34.4%), *Pecari tajacu* (17.0%), *Cuniculus paca* (7.9%), *L. poeppigii* (6.6%), *Tapirus terrestris* (6.3%), and *Mazama americana* (3.9%). During the 180-month study, hunters collected genitalia from 1090 females of the studied species, which was 59.8% of recorded females and equated to the collection of one female genitalia every 5.36 days. Due to the limited accessibility of the study area, researchers could only visit the community once or twice per year. Consequently, samples from the most motivated hunters were used to ensure consistent collection. Hunters recorded all required data from 950 (87.2%) females. Records for 140 (12.8%) females lacked the collection date due to lost or illegible sample codification. We used only genitalia with known collection dates.

The collection of *C. paca* and *L. poeppigii* was significantly seasonal: ($r = 0.2397, p < 0.0001$ and $r = 0.2166$, $p = 0.0177$, respectively). Pregnancy rates within orders were very similar, but varied greatly among orders (Fig. 1 & Table 1). Pregnancy rate in the only sampled carnivore (*Nasua nasua*) was 28.6%, in the 3 studied primates it was 30.9% (SD 6.6), in the 3 artiodactyls it was 42.5% (SD 2.3), in the 2 hystricognath rodents it was 64.7% (SD 2.6), and in the only perissodactyl (*T. terrestris*) it was 74.3%. The average SD of pregnancy rates per species was 8.1% (SD 0.70), and the range was 1.4% (*M. americana*) to 18.9% (*N. nasua*).

The minimum sample size required for a 5% confidence limit ranged from 296 to 374 individuals. However, for a 10% confidence limit, the required sample size dropped to more achievable numbers. Depending on the expected pregnancy rates, required sample sizes for the species we considered ranged from 74 to 94 individuals (Table 2).

For *Lagothrix* sp. and *T. terrestris*, birthrates calculated from our data were similar to those from captive populations (Robinson & Redford 1986) (Table 3). However, reproductive rates were lower from our data on the other ungulates (*T. pecari, P. tajacu*, and *M. americana*) and *C. paca* than from rates widely used in sustainability analyses in Amazonia (Weinbaum et al. 2013) (Table 4). Conversely, *Sapajus macrocephalus*, *Dasyprocta* sp., and *N. nasua* had much higher reproductive rates than those used to calculate commonly used values of $r_{\max}$ (Robinson & Redford 1986). As a result, our $r_{\max}$ calculations were higher than Robinson and Redford's (1986) $r_{\max}$ estimates.

We found no relationship between adult body weight and $r_{\max}$ values calculated by Robinson and Redford (1986) ($r = -0.38$; $r^2 = 0.15$; $p > 0.05$; df = 6; $F = 0.85$). Conversely, we observed a strong relationship between

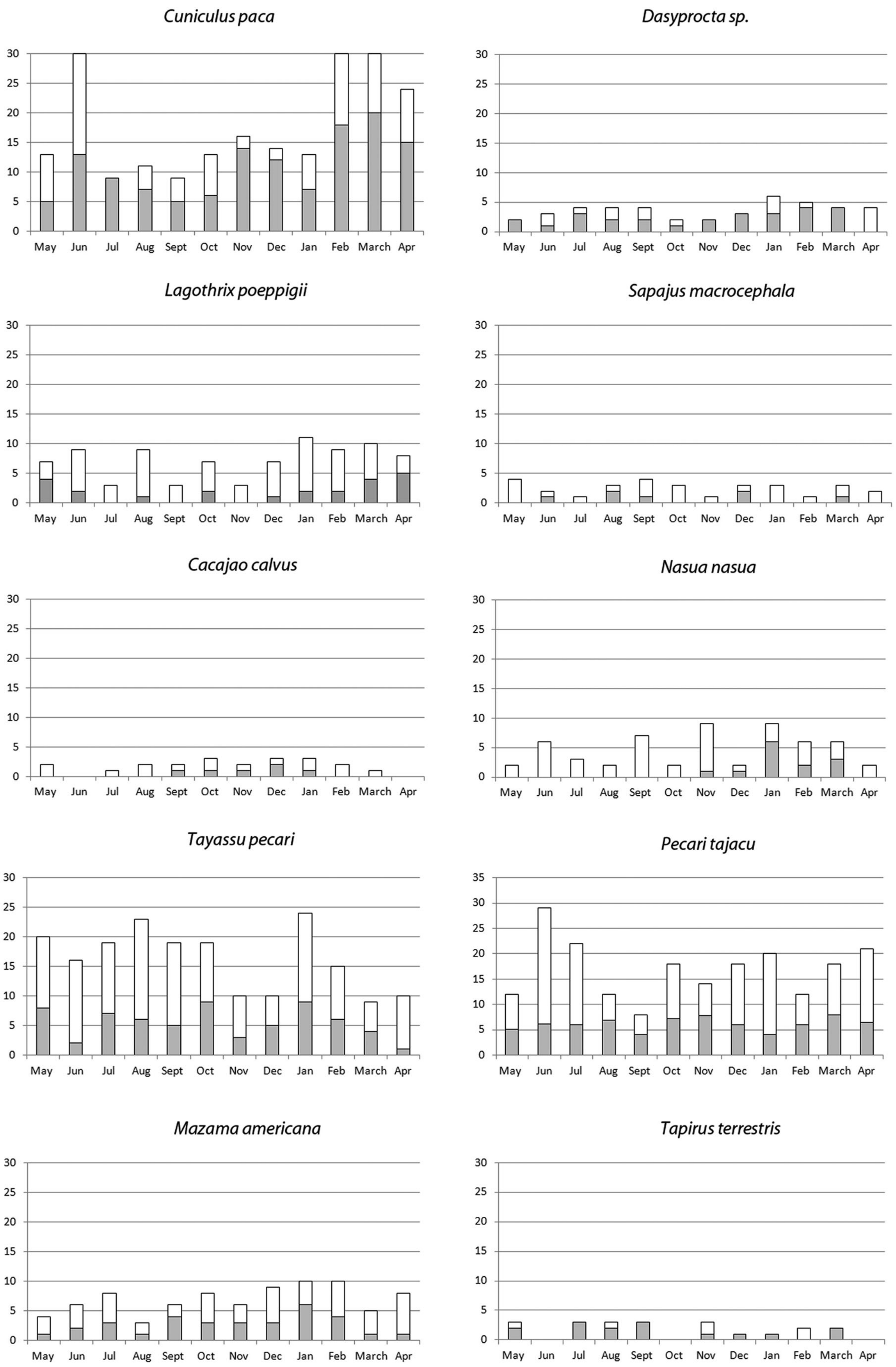

Figure 1. Monthly distribution of pregnant and nonpregnant females in the 10 studied species (white bar, not pregnant; gray, pregnant).

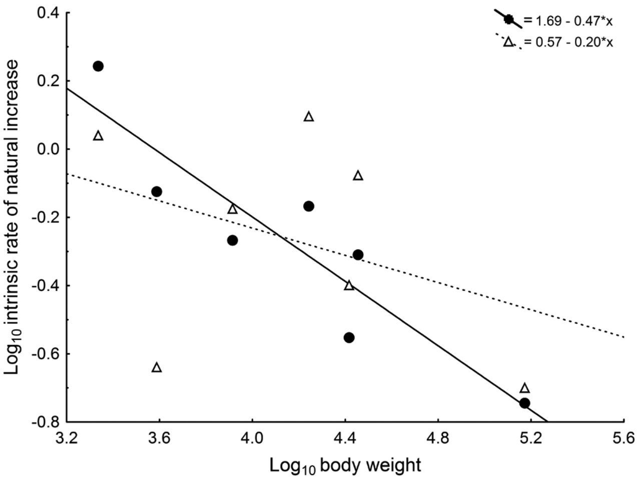

Figure 2. Relationship between the log body weight and the log intrinsic rate of natural increase calculated in this study (filled circles) and by Robinson and Redford (1986) (open triangles) for the 10 most-hunted mammal species in the Peruvian Amazon.

Table 2. Minimum sample size required for a population survey with simple random sampling of expected pregnancy rates for confidence limits of 5% and 10%, a 95% confidence level, and an unlimited population size.

Order	*Expected pregnancy rate (%)*	*Minimum sample size at confidence limit 10%*	*Minimum sample size at confidence limit 5%*
Carnivora	28	77	310
Primates	30	81	323
Artiodactyla	42	94	374
Rodentia	65	87	349
Perissodactyla	74	74	296

body weight and our $r_{\max}$ values ($r = -0.91$; $r^2 = 0.83$; $p < 0.01$; df $= 6$; $F = 25.10$) (Fig. 2).

Discussion

Our sample collection allowed us to estimate reproductive rates for a range of species with divergent life-history strategies. Analyzing the effect of different estimates of annual birthrates on $r_{\max}$ allowed us to assess the effects of the different estimates on sustainability analyses because $r_{\max}$ scales linearly with reproduction. However, ages at first and last reproduction are also estimated from captive populations and may have similar effects. Pregnancy rates varied more among orders than within orders, reflecting shared reproductive strategies in phylogenetically related species.

Cuniculus paca and *L. poeppigii* have seasonal reproductive patterns (Mayor et al. 2013; Bowler et al. 2014), which may not occur in captive breeding systems. These seasonal patterns may remain, even when population sizes are drastically reduced, due to the unknown effects of climate and highly seasonal food availability. Hunters on the Yavari report noticeable fattening of woolly monkeys during the wet season (personal observation), which may indicate that this species uses fat reserves to counter seasonal scarcity of resources. Such seasonal periods of scarcity in which animals operate at a daily calorific deficit are not necessarily eliminated by reduced population levels and may continue to induce seasonal breeding, thus limiting the rate of reproduction a species can achieve in the wild. In using $r_{\max}$, one assumes that hunted populations have unlimited resources which is a questionable assumption for wild populations.

Commonly hunted species such as *T. pecari, P. tajacu, M. americana*, and *L. poeppigii* are often subject to community management plans in which quotas are set and sustainability assessed (Fang et al. 2008). If $r_{\max}$ is used in such assessments, accurate reproductive data are vital to ensure future harvests. Because $r_{\max}$ scales in a linear manner with reproduction, overestimating $r_{\max}$ by 10% may lead to an overestimate of the maximum sustainable yield of 10%. For most hunted species (e.g., *T. pecari, P. tajacu, M. americana,* and *C. paca*), our estimates of wild reproductive rates on the Yavari were considerably lower than the values of $r_{\max}$ that have been widely used for over 30 years and represent a notable decrease of 41.7% and 45.6% in population growth for *T. pecari* and *P. tajacu*, respectively. If the maximum rate of reproduction achievable by these species in the wild is closer to the rates we found on the Yavari than to the traditionally used values of $r_{\max}$, then estimates of maximum sustainable harvest for those studies and in management plans that use the production model (Robinson & Redford 1991) should be greatly reduced. For ungulates, further studies are needed to confirm whether our $r_{\max}$ is in fact near Robinson and Redford's (1986) $r_{\max}$ estimates because possible density-dependent effects may be acting on our estimates (Fang et al. 2008). Although changes to $r_{\max}$ for the *T. terrestris* look small in comparison with Robinson and Redford's (1986) $r_{\max}$ estimates, they still represent substantial changes; thus, overhunting by a small margin would still lead to declining populations in a closed system.

Unlike the commonly used values of $r_{\max}$, our values followed an expected pattern in that they correlated strongly with body weight (Hennemann 1983). This could be considered evidence that our $r_{\max}$ values are consistent with life history and may indicate that large-sized Amazonian mammals have lower-than-expected intrinsic population growth rates under wild conditions.

Robinson and Redford's (1986) production model is largely applied in the tropics because researchers often face data-deficient conditions and the model works with few variables and offers an easy first look at hunting

Table 3. Pregnancy rate, litter size (in fetuses per pregnancy), and yearly reproduction (young per year and per female) from populations of 10 wild mammals in the Amazon region.

Species	Percent pregnancy rate (n)[a]	Litter size (n)[a]	Young/year/ female (n)[a]	Condition	Litter size (n)[b]	Young/year/ female (n)[b]	Reference	Difference between our study and literature (% young/year/ female)
Pecari tajacu	42.6 (204)	1.70 (96)	1.90 (204)	wild	1.93 (41)	2.35 (89)	Gottdenker & Bodmer 1998	-23.7
				captive	1.77 (77)	1.37 (55)	Mayor et al. 2010	+27.9
					1.85 (74)	1.86 (74)	Mayor et al. 2007	+2.1
Tayassu pecari	40.2 (194)	1.64 (89)	1.53 (194)	wild	1.67 (71)	1.23 (219)	Gottdenker & Bodmer 1998	+19.6
				captive				
Nasua nasua	28.6 (56)	4.09 (13)	5.25 (56)	wild	4.61 (31)	4.61 (31)	Hirsch 2007	+12.2
				captive	3–4		Gompper & Decker 1998; Whiteside 2009	
Dasyprocta sp.	66.5 (43)	2.50 (24)	5.54 (43)	wild	2.10 (32)	3.40 (80)	Dubost et al. 2005[c] (*D. leporina*)	+38.6
				captive	1.57	3.68	Guimaraes 2000	+33.6
Lagothrix poeppigii	33.8 (86)	1.00 (27)	0.55 (86)	wild	1.00 (24)	0.33 (13)	Nishimura 2003	+40.0
				captive	1.00	0.55 (139)	Nowak 1999	
							Mooney & Lee 1999	0.0
Cuniculus paca	62.8 (212)	1.02 (139)	1.57 (212)	wild	1.00 (29)	1.8 (29)		-14.6
				captive	1.00 (18)	1.91	Collet 1981	-21.7
						1.62 (18)	Guimarães et al. 2008	+3.2
						1.95	Smythe 1991	-24.2
						2.05	Meritt 1989	-30.6
Mazama americana	44.7 (83)	1.00 (44)	0.74 (83)	wild	1.20 (30)	1.00 (60)	Hurtado-Gonzales & Bodmer 2006	-35.1
				captive				
Tapirus terrestris	74.3 (21)	1.00 (17)	0.68 (21)	wild	1.00 (10)	0.73 (13)	Pezo et al. 2004	-7.4
				captive	1.00	0.67	Pukazhenthi et al. 2013	+1.5
Cacajao calvus	35.7 (21)	1.00 (6)	0.85 (21)	wild				
				captive				
Sapajus macrocephalus	0.233 (30)	1.13 (8)	0.63 (30)	wild	1.00	0.63	Fragaszy & Adams-Curtis 1998	-14.3
				captive	1.02		Leighty et al. 2004	

[a] *Data obtained from our study of wild populations in the Yavari-Mirin River.*
[b] *Data obtained from other studies, both from wild and captive populations.*
[c] *Dubost et al. (2005) used a 117-day gestation length, whereas we used 149 days (Guimaraes et al. 1997).*

Table 4. Reproductive parameters and $r_{\max}$ calculated from data collected from wild animals (this study) and from animals in captivity (Robinson & Redford 1986).

Species (taxonomy used in Robinson & Redford 1986)	*Age at first reproduction (Robinson & Redford 1986)*	*Annual birth rate of female offspring (Robinson & Redford 1986)*	*Annual birth rate of female offspring (this study)*	*Age at last reproduction (Robinson & Redford 1986)*	*r_{max} (Robinson & Redford 1986)*	*r_{max} (this study)*	*Percent difference between r_{max} of Robinson and Redford (1986) and this study*
Brown capuchin, *Sapajus macrocephalus* (*Cebus apella*)[a]	5	0.27	0.35	25	0.14	0.16	+14.3
Woolly monkey, *Lagothrix poeppiggii (Lagothrix lagothricha)*	5	0.29	0.26	20	0.14	0.13	-7.1
Red uakari monkey, *Cacajao calvus*	3.5[a]	n/a	0.36	23[a]	n/a	0.08	n/a
Collared peccary, *Pecari tajacu*	0.9	2.20	0.91	13	1.25	0.68	-45.6
White-lipped peccary, *Tayassu pecari*	1.5	2.00	0.80	13	0.84	0.49	-41.7
Red brocket deer, *Mazama Americana*	1.10	0.95	0.37	8	0.40	0.28	-30.0
Lowland tapirm *Tapirus terrestris*	3.7	0.38	0.34	23.5	0.20	0.18	-10.0
Paca, *Cuniculus paca (Agouti paca)*	1	0.95	0.71	12.5	0.67	0.54	-19.4
Black agouti, *Dasyprocta* sp. *(Dasyprocta leporina)*[b]	0.74	0.75	3.02	10	1.10 (0.63)[c]	1.75	+59.1 (+177.8)
South American coati, *Nasua nasua*	2.5	0.50	2.69	7	0.23	0.75	+191.3

[a] *Data for Sapajus sp. used (Hayes et al. 1972; Wright & Bush 1977).*

[b] *We compare Dasyprocta sp. with D. leporina because parameters for D. leporina (Robinson & Redford 1986) have been widely applied to populations of other species.*

[c] *Robinson and Redford (1986) contained an error for Dasyprocta in which either the parameters have been misprinted or r_{max} was miscalculated, we present r_{max} calculated from their given parameters in parentheses.*

sustainability in an area. Other studies of the sustainability of subsistence hunting have also relied on basic reproductive data or $r_{\max}$, such as source-sink models (e.g., Joshi & Gadgil 1991), spatial models (e.g., Levi et al. 2011), and agent-based models (e.g., Iwamura et al. 2014). Results of such studies often form the basis for management and conservation decisions.

We suggest that calculating $r_{\max}$ from captive data appears unreliable because the results obtained do not correlate with body mass, a well-established relationship (e.g., Fenchel 1974; Blueweiss et al. 1978; Hennemann 1983). Furthermore, $r_{\max}$ may not be an appropriate measure for *T. pecari, P. tajacu*, *M. americana*, and *C. paca* because we found very different reproductive rates in our wild, hunted populations. Estimates of maximum population growth possible should be more conservative to avoid setting hunting quotas that lead to overharvesting. Furthermore, previous values of $r_{\max}$ for *Dasyprocta* sp. and *N. nasua* are likely to be incorrect. For these species, we found higher annual birthrates of female offspring (parameter b in the $r_{\max}$ calculation) on the Yavari than those presented by Robinson and Redford (1986), and our new values are more consistent with the life history of these species. Because birthrate is expected to be related to body size, it is improbable that *Dasyprocta* sp. and *N. nasua* have lower values for this parameter than species that are more than twice as large, such as *C. paca* and *Panthera onca* respectively, as estimated by Robinson and Redford (1986). We suggest the birthrates we calculated should be used to calculate $r_{\max}$ and that these values are likely far more accurate than historically used values. In some cases, Robinson and Redford's (1986) $r_{\max}$ will be the same as our $r_{\max}$ (Table 4). However, the ideal course of action is to derive reproductive parameters from the local populations at which sustainability studies are conducted (Miller-Gulland & Akçakaya 2001). These parameters could be used in analyses that do not require $r_{\max}$ or to verify that wild reproductive rates are realistic, as we did here.

Although a few species (e.g., *N. nasua*) are monoestrous and only physiologically capable of reproducing once per year (Mayor et al. 2013), most should be considered opportunist seasonal breeders capable of breeding year-around when sufficient food is available (Mayor et al. 2011). As well as seasonal differences, this may also result in variable interannual reproductive efficiency. Seasonal and interannual variations in reproduction affect estimates of pregnancy rate if the sample collection is not both homogenously distributed year-around and spread over a number of years. In our study, only *L. poeppigii* and *C. paca* were sampled in a seasonal distribution differing significantly from random, but low sample sizes may hide subtle seasonal biases. Our samples were not distributed homogenously throughout the year, and while it is possible to control for seasonal differences by taking the average of monthly reproductive rates or the average of wet and dry season reproductive rates, this would require larger sample sizes.

Implementing Participatory Sampling of Reproductive Organs

Our sample-collection method was integrated into a communal participatory program aimed at improving the conservation and sustainability of natural resources and livelihoods of human communities. Collection of genitalia from hunted wild animals by local people allows the examination of reproduction in wild populations in natural habitats without impractical direct observation and without taking samples additional to those normally harvested.

In our study area, local people normally discard thoracic and abdominal organs, including female genitalia. Therefore, the collection of the biological samples is compatible with the local culture. Nevertheless, training is required to properly remove organs, safely preserve in 4% formaldehyde solution (v/v), and register all hunted animals with a code related to the respective biological sample. We did not observe significant difficulty in the collection and the conservation of biological samples, but the project had no direct funds, which limited regular monitoring of the sample collection. Thus, we focused efforts on self-selected and motivated hunters.

Sample sizes were not sufficient for 10% confidence levels (74–94 individuals) for *Dasyprocta* sp., most primates, and *T. terrestris*, and they were marginally sufficient for *M. americana*. Sufficient sample sizes are probably achievable in most areas, given that the species of most interest in terms of managing hunting are likely to be sampled most frequently by hunters. However, if confidence limits of 5% are required, achieving the minimum range of sample size of 296–374 individuals would likely require many more years of sample collection or additional sampling strategies directed at improving participation of local hunters.

In our study, researchers were responsible for the dissection of the genitalia, but we believe that it is possible to train hunters to determine accurately the pregnancy state of any hunted individual on their own, although the difficulty of detecting very early pregnancies with small fetuses would need to be factored in. The first anatomical signs of pregnancy are observed around the 15th day of gestation (Mayor et al. 2005), but we noticed that hunters may have problems diagnosing pregnancy until the 30th day of pregnancy. If hunters could identify pregnancy in the field without preservation of organs, then collections would be cheaper and more frequent and the need for storage space and transportation of samples from remote kill sites would be eliminated. The resulting increase in sample size would allow more accurate estimations of pregnancy rates, provide greater confidence in monthly pregnancy rates, and remove bias due to the seasonal data collection. Larger sample sizes would also allow the observation of changing reproductive rates between years.

We estimated that our project cost US$200/year and $2.75/biological sample, excluding costs related to access to the study area. Hunters were not paid for collection. Our simple, low-cost method allows for the efficient collection of a great diversity of wild species and focuses on the most frequently hunted species with the most need for reproductive data and management strategies. The use of our data-collection method and the appropriate use of reproductive parameters in community wildlife management could improve the conservation and sustainable use of natural resources and consequently the quality of life for rural communities.

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