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Breeding seasonality in the lowland paca (*Cuniculus paca*) in Amazonia: interactions with rainfall, fruiting, and sustainable hunting

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The resilience of a given species to hunting is conditioned by the effect of potential threats upon the more sensitive periods in its life history, such as when animals are breeding. We investigated the environmental drivers of breeding seasonality in the lowland paca (*Cuniculus paca*), and the potential impact of hunting on the species. As part of a participative study with hunters in 2 Amazonian sites, we obtained reproductive organs of pacas as well as information on the hunters' daily wild meat extraction. Using data on rainfall, river water level, and fruiting phenology from the 2 study sites, we applied generalized additive models for location, scale, and shape (GAMLSS) to examine the effect of climatic and environmental factors on paca reproduction. Forest fruiting was directly linked to higher pregnancy rates in pacas, and when lactation and weaning of offspring mostly occurred. Hunting was highly seasonal in all studied years and positively correlated with higher levels of river water. The coincidence between hunting patterns and paca reproductive cycles during the wet season resulted in more pregnant females being harvested. In addition to the known slow reproductive rate of pacas, the disproportionate offtake of pregnant females may affect the long-term sustainability of hunting of this species. Reducing hunting during the flooded season may not be feasible because the lowland paca provides most of the wild meat consumed by thousands of rural Amazonians during this period. However, options to offset the negative effects of killing of pregnant females could include the zoning of hunting areas or encouraging hunters to target primarily males. Our results indicate that strategies for the sustainable harvest of pacas and other heavily hunted Amazonian mammals should consider the interaction between the species' reproductive cycles and hunting by local people in order to enhance conservation and management efforts.

A resiliência de uma espécie à caça é condicionada pela sua capacidade reprodutiva intrínseca e pelo efeito de potenciais ameaças durante os períodos mais sensíveis de sua história de vida, como o período reprodutivo. Neste trabalho, nós investigamos os fatores ambientais que determinam a sazonalidade reprodutiva da paca

(*Cuniculus paca*) e o potencial impacto da caça sobre a espécie. Em um estudo participativo de 15 anos em duas áreas da Amazônia, obtivemos órgãos reprodutivos de pacas doados voluntariamente por caçadores, bem como informações sobre seus padrões diários de caça. Usando informações sobre precipitação, nível d'água dos rios e fenologia de frutificação, nós aplicamos modelos aditivos generalizados (GAMLSS) para examinar o efeito de fatores climáticos e ambientais na reprodução da paca. A precipitação esteve positivamente ligada a uma maior frutificação, que por sua vez foi correlacionada com maiores taxas de prenhes da paca e com os períodos de lactação e desmame da prole. A caça de paca foi altamente cíclica ao longo dos anos e positivamente associada aos níveis d'água mais elevados. A convergência entre os padrões de caça e os ciclos reprodutivos de paca resulta na extração de um grande número de fêmeas grávidas. Juntamente com a lenta taxa de reprodução da espécie, a captura desproporcional de fêmeas grávidas pode afetar a sustentabilidade do uso da paca. Reduzir a caça durante os períodos de inundação pode não ser viável, pois a paca é a espécie responsável por fornecer grande parte da carne silvestre consumida por milhares de moradores rurais da Amazônia neste período. No entanto, ações para compensar os efeitos negativos da extração de pacas grávidas poderiam incluir o zoneamento de áreas de caça ou o incentivo aos caçadores em abater preferencialmente machos. Nossos resultados indicam que estratégias para a extração sustentável da paca e outras espécies cinegéticas amazônicas devem considerar a interação entre a reprodução e a caça pela população local, a fim de melhorar as ações de conservação e manejo no bioma.

Key words: conception dates, forest phenology, game species, hunter participation, management, pregnancy rates, rainfall patterns, reproduction, Rodentia, wildlife

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In high latitudes, where climatic variability between seasons is greatest, most species produce a large number of offspring in a short period of time, most of which do not survive (Bronson 1985). By contrast, in more stable environments with less seasonal variation, such as tropical forest regions, species generally produce a constant, low number of offspring over the year (McNaughton 1975). However, in the Amazon basin, the extreme variation in river levels, caused by seasonal meltwater in the Andes or rainfall, affects food availability (particularly tree fruits) to such an extent that frugivorous mammals may exhibit a greater than expected reproductive seasonality for this environment (Dubost et al. 2005). Furthermore, seasonal patterns in water levels also determine patterns of hunting and fishing by humans (Endo et al. 2016).

Animal populations are regulated by factors that impact mortality and recruitment (Caughley 1977). Understanding the population dynamics of exploited species is essential to determine sustainable harvest rates for wildlife populations. Harvesting individuals can have direct effects on the growth rate of a population by increasing mortality rates. There is increasing evidence that harvesting can also have indirect effects on population growth. For instance, harvest can disrupt the sex and age structure of a population, which can in turn affect fecundity rates (Milner et al. 2007; Bunnefeld et al. 2009). Furthermore, sex-skewed harvesting can have potentially deleterious effects on long-term fecundity (defined as the number of young born) and lead to population collapse, as shown for ungulates (Ginsberg and Milner-Gulland 1994; Freeman et al. 2014). In addition, overhunting of females in seasonally breeding animals, during periods when more females are pregnant, may negatively influence the population dynamics of the species.

In this paper, we evaluate how hunting may affect the population dynamics of the lowland paca (*Cuniculus paca*). The paca is a large, frugivorous caviomorph rodent that occurs throughout the Neotropics, inhabiting primarily broadleaf forests from east-central Mexico to northern Argentina (Collet 1981; Pérez 1992; Aquino et al. 2009). Studies to date, in primary broadleaf forest, suggest that pacas occupy relatively small home ranges (Marcus 1984; Beck-King et al. 1999), and are patchily distributed in mosaic landscapes with scattered resources (Marcus 1984; Beck-King et al. 1999; Ulloa et al. 1999). Pacas feed mostly on fruits and seeds, and occasionally consume leaves and flowers (Beck-King et al. 1999; Dubost 2017).

Pacas are of conservation and management interest throughout their geographic range as a popular game species for people (e.g., Read et al. 2010; El Bizri et al. 2015, 2016; Gutiérrez-Granados 2015; Mayor et al. 2015), an important prey of large carnivores, and as seed dispersers (Dubost and Henry 2006; Aquino et al. 2009). However, there is concern that current levels of hunting may be unsustainable, as observed in several Amazonian sites (e.g., Zapata-Ríos et al. 2009; Valsecchi et al. 2014). Given the importance of the paca as a source of protein to human residents of tropical forests, identifying the factors that may affect paca numbers remains fundamental.

Here, in 2 sites in Amazonian Peru and Brazil, we first assess how environmental factors such as rainfall patterns affect fruit availability, and in turn show how this correlates with the reproductive seasonality of pacas. We then assess the impact of harvest rates during the different phases of the reproductive cycle of pacas using data gathered from a 15-year participatory hunting study for the 2 study sites.

Materials and Methods

Study sites.—The Yavarí-Mirín River (YMR; 04°19′53″S, 71°57′33″W) is located in the western Peruvian Amazon, encompassing 107,000 ha of continuous upland forests containing a single indigenous community of 307 inhabitants (Fig. 1). The Amanã Sustainable Development Reserve (ASDR; 01°54′00″S, 64°22′00″W) is a 2,313,000-ha reserve of predominantly upland

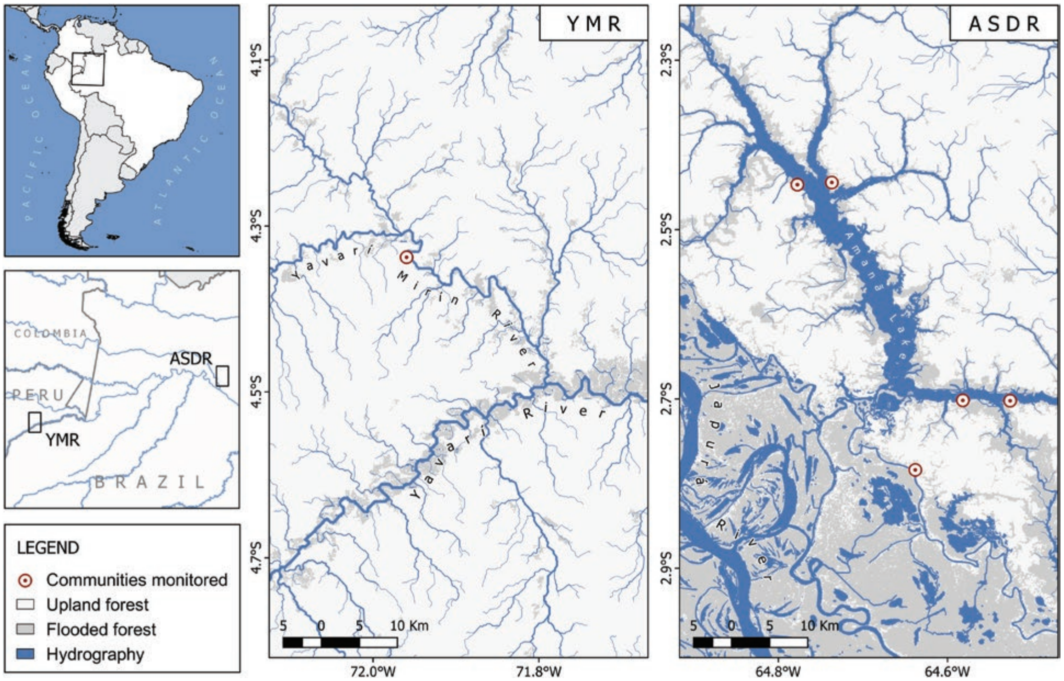

Fig. 1.—Location of the 2 study sites (YMR: Yavarí-Mirín River, ASDR: Amanã Sustainable Development Reserve) in Amazonia and the communities participating in the monitoring of hunting and collection of biological material on lowland pacas (*Cuniculus paca*).

forests in the central Brazilian Amazon, between the Negro and Japurá rivers. Approximately 4,000 riverine people inhabit 23 communities and some isolated settlements within this reserve (Fig. 1). In both study sites, local communities rely on agriculture for income and on hunting and fishing for subsistence. River water levels at both sites change seasonally, varying up to 12 m between the dry and flood peaks (Ramalho et al. 2009). Climate in both study sites is typically equatorial with annual temperatures ranging between 22°C and 36°C, relative humidity of 80%, and an annual rainfall of 1,500–3,000 mm.

Water level and rainfall.—For the YMR, we calculated monthly average river water level (as meters above sea level—m a.s.l.) and rainfall (in mm) on the Yavarí River, from data provided by a Brazilian National Water Agency hydrological station, ca. 50 km from the study site (HidroWeb, Estirão do Repouso station, rainfall: 1962–1999, water level: 1980–2017, http://www.snirh.gov.br/hidroweb/). In the ASDR, we used data on average rainfall (mm) for the Tefé municipality, ca. 90 km from the study area, from information also provided by the Brazilian National Water Agency (HidroWeb, Tefé station, 2005–2017, http://www.snirh.gov.br/hidroweb/). We used data on river water levels from the Mamirauá Sustainable Development Institute for the Amanã Lake station inside the ASDR (1990–2018, https://mamiraua.org.br/pt-br/pesquisa-e-monitoramento/monitoramento/fluviometrico/).

Ripe fruit availability.—We determined annual changes in ripe fruit availability, the main item in the diets of pacas (Dubost et al. 2005), by monitoring tree fruit abundance in 3 transects between March 2004 and February 2005. Two transects, started at random points, were in upland forests in the YMR, and a third transect was located in *aguajal*, upland swamp forest dominated by palms. Two transects were 5 m wide and one in the upland forest was 20 m wide (Pitman et al. 2003). We tagged and identified every tree of a diameter at breast height (DBH) > 10 cm, as well as every vine or liana of DBH > 7 cm (Ayres 1986). We marked plants until the rate of discovery of new species plateaued (Sutherland 2000), which determined the length and area of each transect. Starting mid-month, we observed the canopy of each tagged tree or vine once per month with binoculars and a small telescope, recording the presence or absence of ripe fruits in each sampled individual plant. Because fruits of the moriche palm (*Mauritia flexuosa*) constitute an important part of the diet of pacas (Mendieta-Aguilar et al. 2015), we also obtained more detailed fruiting data from the 38 individuals found within the transects and analyzed it independently.

Paca reproduction and hunting.—We trained local hunters in the YMR community and in 5 ASDR communities to remove all abdominal and pelvic organs from harvested specimens and to store these materials in buffered 4% formaldehyde solution (Mayor et al. 2017). From 2000 to 2015, local hunters collected and voluntarily donated genitalia from 300 female pacas (212 in the YMR and 88 in the ASDR), each labeled with the hunting date. Since hunters do not consume these organs, we avoided encouraging additional mortality to supply our study. In parallel, between 2000 and 2015 in the YMR, and between 2002 and 2015 in the ASDR, hunters recorded all harvested pacas, including sex and hunting date. In each monitored community in YMR and ASDR, local hunters were provided with datasheets in which they voluntarily recorded information on their daily hunting events. To ensure data were accurately collected, we conducted regular workshops and meetings (at least once per year) with all data providers and members of the participating communities. In this study, we only used the data for harvested females.

Data analysis.—We removed the conceptuses from all pregnant females. Using a metal caliper (maximum 300 mm) and a tape measure (1.0 mm accuracy), we measured the crown-rump length and longitudinal length of each embryo or fetus, from rostral edge of nose to distal portion of the tail. Conception dates were determined by backdating the date of collection of each embryo or fetus from their estimated age, using the age formula for paca fetuses in El Bizri et al. (2017). Predicted parturition dates were estimated by summing a standard gestation length of 149 days (Guimarães et al. 2008) to the derived conception dates. We then calculated the monthly number and percentage of conceptions and parturitions during the study period. Hunting data on females collected by local people were also used to calculate the monthly percentage of female pacas harvested in each site within each monitored year (hereafter known as hunting rates). Additionally, we estimated the pregnancy period (from conception to parturition dates) for each paca, and summed the cumulative number of pregnant pacas per month to obtain a monthly percentage of pregnant females among all collected samples in a year (hereafter known as pregnancy rate). We also estimated the monthly percentage of weaned offspring by summing a standard lactation length of 21 days to the parturition dates, which correspond to the period after which the offspring, although still suckling, starts eating solid food (Collett 1981). In addition, we calculated the average longitudinal length of the embryos or fetuses in each locality.

We applied generalized additive models for location, scale, and shape (GAMLSS—Stasinopoulos and Rigby 2007) to assess the relationship between climate, fruiting, paca reproductive events, and hunting. By using GAMLSS, it is possible to test across a wide set of distribution families, ensuring the best fit to the data is selected. Analyses were conducted in 3 sets using a theoretical framework of likely direct relationships between the variables. In set (1), we evaluated the relationship between monthly rainfall (predictor variable) and monthly fruiting percentage in the 3 YMR environments. In set (2), we evaluated the relationship between monthly fruiting percentage in the 3 environments (predictor variables) and paca reproductive events (percentage of conceptions, parturitions, and weaning, and pregnancy rates) for the YMR; in this second set, we also tested rainfall as a predictor variable for conceptions in both areas (YMR and ASDR), since this factor has been reported as a possible cue for conceptions in several mammal species. In set (3), we evaluated the relationship between river water level and paca reproductive events (predictor variables) with hunting rates. For the latter, we calculated the monthly percentage of harvested females in each year in both areas and related these values with the monthly average water level and percentage reproductive events, which were considered constants among months, independently of the year.

We tested all combinations of predictor variables in each set in linear or nonlinear forms using different distribution families. Final models were selected based on ΔAIC values, i.e., the difference between the value of Akaike's information criterion (AIC) for the model being evaluated and the model with the lowest AIC value (Burnham and Anderson 2004); ΔAIC values smaller than 2 indicated models with good support. Among these models, we chose the simplest one as final, i.e., the model with fewest degrees of freedom and with fewest predictor variables in the model. We used R 3.3.3 software (R Core Team 2017) for all statistical analyses. GAMLSS were run using the *gamlss* R-package. Values are expressed as the mean ± standard deviation ($\bar{X} \pm SD$).

Compliance.—All research followed guidelines of the American Society of Mammalogists for the ethical use of wild animals in research (Sikes et al. 2016) and was conducted in compliance with the research protocol approved by the Research Ethics Committee for Experimentation in Wildlife at the Dirección General de Flora y Fauna Silvestre from Peru (License 0229-2011-DGFFS-DGEFFS), by the Instituto Chico Mendes for Biodiversity Conservation from Brazil (License SISBIO No. 29092-1), and by the Committee on Ethics in Research with Animals of the Federal Rural University of the Amazon (UFRA CEUA protocol 007/2016).

RESULTS

Ripe fruit availability.—We sampled 589 trees and vines in 8,970 m^2 of upland forests, and 386 trees and vines in 5,150 m^2 of swamp forests. Fruiting patterns in the YMR varied according to habitat type. In upland forests, fruiting trees were present throughout the year, with peaks in March (6.62% plants fruiting) and December (4.68% plants fruiting; Fig. 2). In swamp forests, fruiting peaked between February and May (6.12 ± 0.83% plants fruiting), with no trees fruiting in September and October. *Mauritia flexuosa* showed marked fruiting during the low rainfall period (May–August), with the highest number of fruiting trees recorded in June (34.21%); no fruits were observed during the remaining months of the year (Fig. 2). Upland forest fruiting was positively correlated with rainfall (Fig. 3; Table 1), but there was no correlation between rainfall and *M. flexuosa* or swamp forest fruiting (Table 1).

Paca reproductive seasonality.—There were 157 (52.3%) pregnant pacas among all sampled females, 100 (47.2%) in the YMR and 57 (64.8%) in ASDR (Fig. 4). Average fetal length was 11.30 ± 10.58 cm in the YMR and 17.43 ± 9.74 cm in the ASDR, with a significant difference between sites ($t_{155} = 3.59$, $P < 0.01$). Paca reproductive events occurred during different periods of the year in the 2 study sites. In YMR, conceptions occurred mainly between October and January (50.0%), while parturitions primarily took place between March and June (49.0%). In ASDR, most conceptions occurred between March and June (45.6%), while most parturitions happened between August and November (42.1%; Fig. 5). Nevertheless, conceptions and parturitions occurred throughout the year in both sites. There was a positive relationship between conceptions and rainfall in both study sites (Figs. 6A and 6B), but there was a negative relationship between conceptions and fruiting in upland forests in the YMR (Fig. 6C; Table 1). Pregnancy rates were positively associated with fruiting in upland forest (Fig. 6D), while the higher weaning rates were

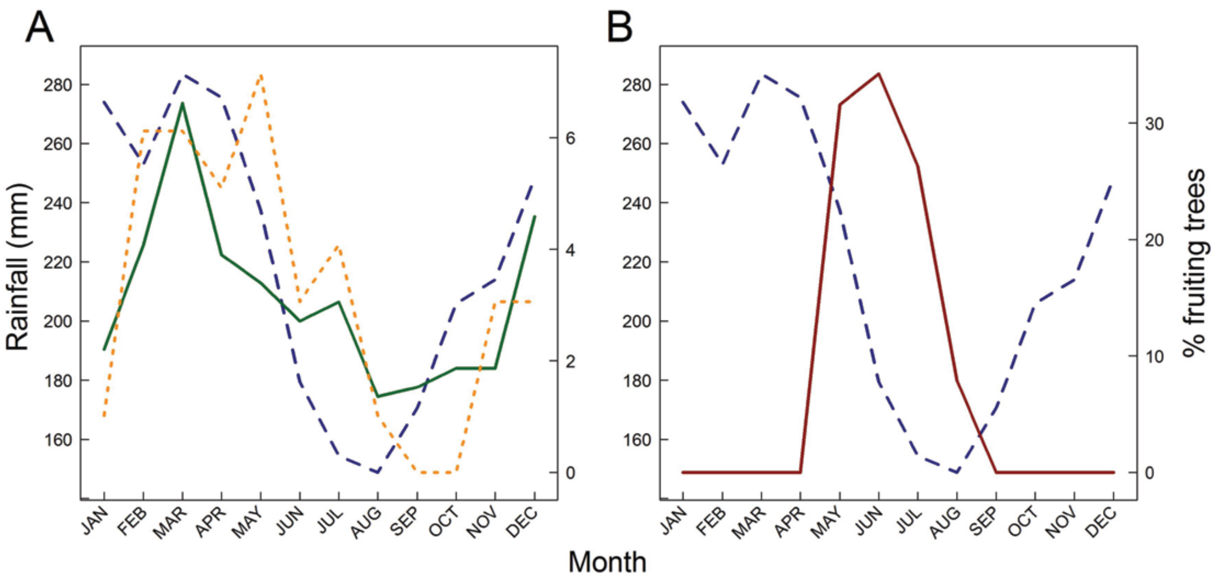

Fig. 2.—Trends in (A) rainfall (dashed line) and percentage of trees bearing fruits in upland forests (solid line) and swamp forest (dotted line); and (B) rainfall (dashed line) and percentage of *Mauritia flexuosa* trees bearing fruits (solid line) along the year in the Yavarí-Mirín River, western Amazonia.

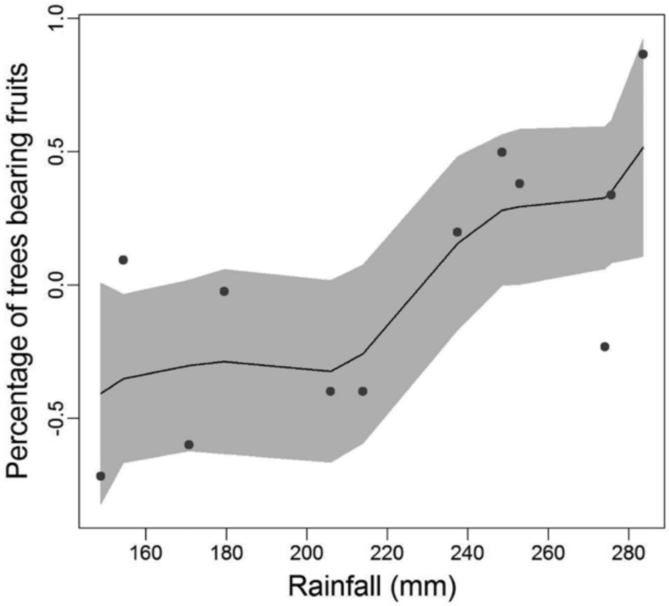

Fig. 3.—Relationship between rainfall (mm) and percentage of trees bearing fruits in upland forests in the Yavarí-Mirín River, western Amazonia. The gray area represents 95% *CI*s. The response variable is plotted on the y-axis in a scale of variation around the mean (μ = 0) calculated from the original data used to build the model.

related to higher fruiting periods in swamp forest (Fig. 6E) and of *M. flexuosa* (Fig. 6F; Table 1). On the other hand, there was no relationship between parturition and fruiting in any environment (Table 1).

Hunting vulnerability of pregnant pacas.—A total of 803 harvested paca females were recorded in the communities, 288 in the YMR and 515 in the ASDR. Hunting rates varied between months, which were cyclical along the years (Figs. 7A and 7B) and showed a positive relationship with the river water level in both study sites (Figs. 7C and 7D; Table 1). A strong positive relationship between hunting rates and pregnancy rates was observed (Figs. 7E and 7F; Table 1). There were no relationships between conceptions, parturitions, and weaned offspring and hunting rates (Table 1).

DISCUSSION

Paca reproductive seasonality and fruit availability.—Although pregnant females were present year-round in our study sites, most pregnancies occurred during periods of greater fruit availability in upland forests, when rainfall was highest. The greater food supply during this period can sustain larger numbers of pregnant females. When most females are in their last third of gestation, a period of greatest absolute fetal growth and when pregnant individuals demand more energy, fruit availability is, in fact, at its peak. A similar pattern has been observed for the ring-tailed coati (*Nasua nasua*) where the gestation period, concentrated between November and March, coincided with greater fruit availability in upland and swamp forests in the YMR (Mayor et al. 2013a). However, mammals with less selective diets are aseasonal breeders, as in the case of the white-lipped peccary (*Tayassu pecari*), collared peccary (*Pecari tajacu*), and the red brocket deer (*Mazama americana*—Mayor et al. 2009, 2010, 2011), because these species consume green leaves, insects, and small vertebrates when fruit is less available (Dubost and Henry 2017). This pattern has also been confirmed by Dubost and Henry (2017) in French Guiana, who showed that mammals that consume more fruits were highly seasonal breeders.

Changing energy demands and seasonality in food supply.—There is evidence from Amazonia that a seasonal increase in rainfall triggers fruit maturation in several habitat types, including nonflooded forests (Haugaasen and Peres 2005). Since rainfall and river water levels vary in different regions of the

Table 1.—Details of the best-fit models using GAMLSS for each response variable, with the family of distribution, ΔAIC in relation to the null model (ΔAIC null), and generalized R^2. Nonlinear effects were fit using cubic spline (*cs*) functions provided by *gamlss* R-package. Families of distributions are represented by log-normal (LOGNO), normal (NO), zero-adjusted gamma (ZAGA), gamma (GA), Box–Cox t (BCTo), inverse Gaussian (IG), Gumbel (GU), inverse gamma (IGAMMA), and reverse Gumbel (RG). Generalized R^2 were calculated using the function Rsq of the *gamlss* package. Null models are indicated by 1. GAMLSS: generalized additive models for location, scale, and shape.

Best-fitted model[a]		Estimate	*P*-value	Family of distribution	ΔAIC null	Generalized R^2
Response variables	Predictor variables					
Yavarí-Mirín River						
Fruiting						
% Plants fruiting U.F.	*cs*(rainfall)	0.0068	0.011	LOGNO	5.45	62.0
% Plants fruiting S.F.	1			NO	0	
% Plants fruiting *M.f.*	1			ZAGA	0	
Paca reproductive events						
% Conceptions	Rainfall	0.0083	0.011	LOGNO	3.97	48.5
	% Plants fruiting U.F.	−0.2147	0.027			
% Parturitions	1			IG	0	
% Weaned offspring	% Plants fruiting S.F.	0.6945	0.009	GU	11.95	73.5
	% Plants fruiting *M.f.*	0.0972	0.041			
Pregnancy rate	*cs*(plants fruiting U.F.)	0.0734	0.007	IGAMMA	5.60	67.0
Paca hunting						
Hunting rates	Water level	0.0541	0.033	ZAGA	6.02	6.7
	Pregnancy rate	0.2239	0.003			
Amanã Reserve						
Paca reproductive events						
% Conceptions	*cs*(rainfall)	0.0333	0.001	RG	3.97	53.6
Paca hunting						
Hunting rates	Water level	0.1020	< 0.001	ZAGA	7.22	29.1
	Pregnancy rate	0.2223	< 0.001			

[a] Abbreviations for plants fruiting—U.F.: upland forest; S.F.: swamp forest; *M.f.*: *Mauritia flexuosa*.

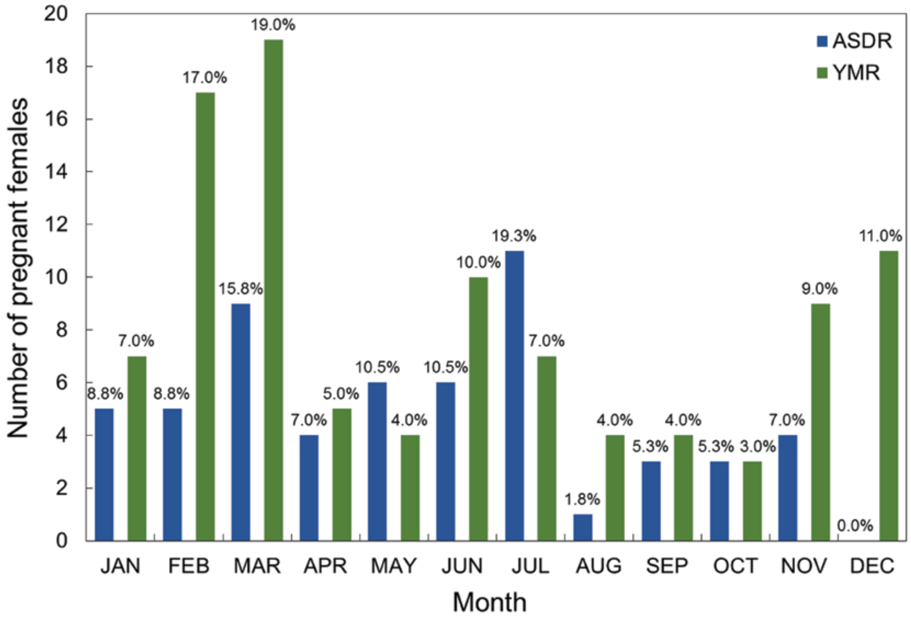

Fig. 4.—Number and percentage of lowland paca (*Cuniculus paca*) samples that included a uterus showing signs of pregnancy, collected in each month over the monitoring years in the Amanã Sustainable Development Reserve (ASDR) and Yavarí-Mirín River (YMR), Amazonia.

Amazon, reproductive events of the paca occur at different phases of the year in each of our studied sites, according to local variations in climate and fruit production. Paca reproduction is therefore plastic and opportunistically seasonal (Mayor et al. 2013b). Thus, for fruit-dependent species, rainfall, in contrast to photoperiod, may drive conceptions to take place some months prior to fruit ripening, and pregnancies and births will coincide with the period of higher fruit abundance. The observation made by Dubost and Henry (2006) that nonpregnant pacas consumed less seeds than pregnant animals also suggests that conceptions occur during periods of low food availability so that pregnancies mostly occur during periods of higher

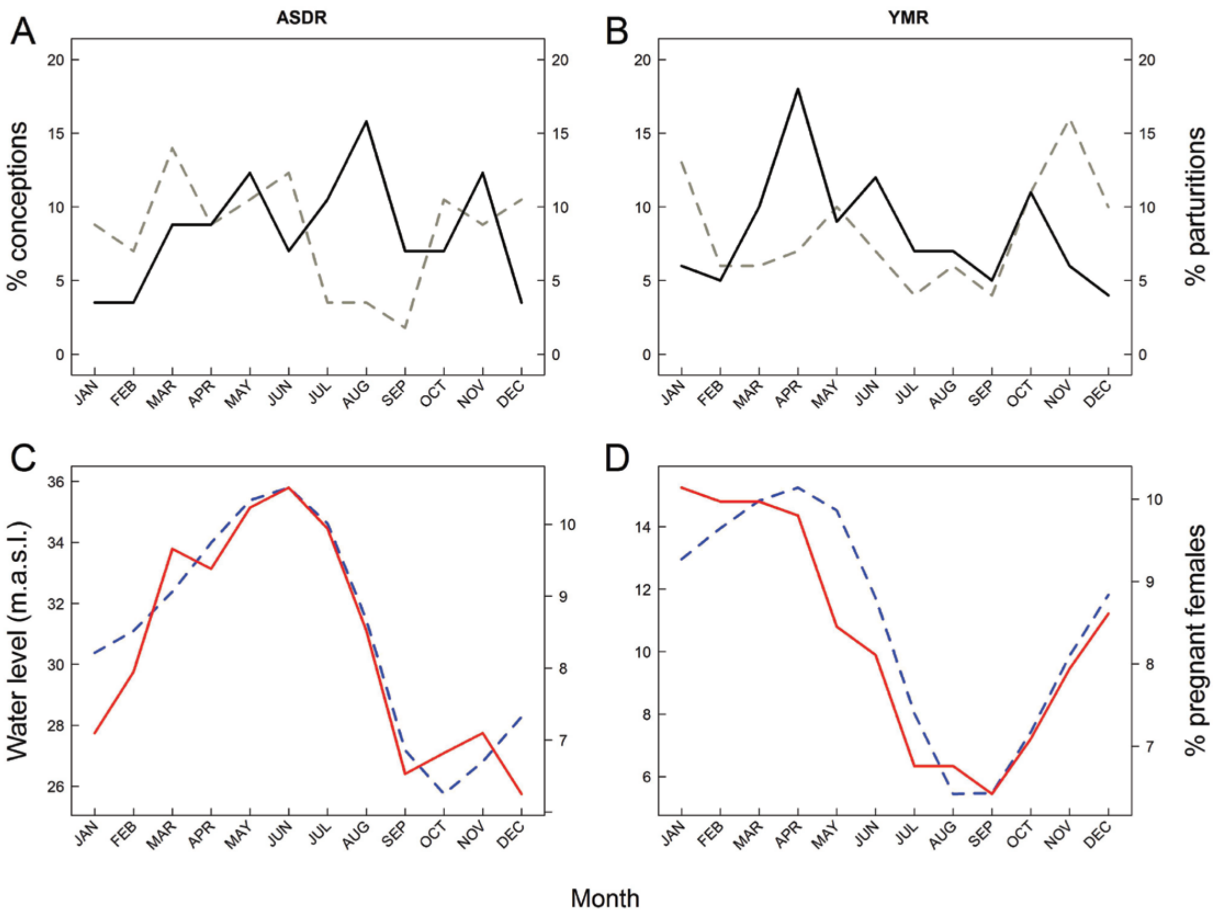

Fig. 5.—Trends in (A and B) the percentage of paca conceptions (dashed gray lines) and parturitions (solid black lines); and (C and D) average river water level (dashed lines) and percentage of pregnant female pacas (solid lines) along the year in the Amanã Sustainable Development Reserve (ASDR) and Yavarí-Mirín River (YMR), Amazonia.

fruit and seed availability. Our results also show that the greatest number of conceptions occurred when fruit availability in upland forests was low; pregnant pacas could take advantage of the subsequent periods of greater food supply. Similarly, in free-ranging, provisioned rhesus macaques (*Macaca mulatta*) on islands in Puerto Rico, more conceptions occurred during the spring rainfall period, just before the main tree-fruiting season (Rawlins and Kessler 1985).

In Amazonia, swamp forest species and *M. flexuosa* in particular (the most important source of food during the drought period) play a major role in sustaining lactating females and their young, which start weaning during the low-water period. Since during lactation females consume up to 5 times more food than before pregnancy (Randolph et al. 1977), the availability of ripe fruits during this period is of extreme importance. For several species of flying foxes (*Pteropus* spp.), O'Brien (1993) showed that lactation and offspring weaning occur during periods when fruit supply is at its peak. In addition, Lee et al. (2017) showed that giraffe (*Giraffa camelopardalis*) calves born during the dry season in Tanzania had a higher survival probability due to the greater energy reserves accumulated by mothers during the rainy season as well as the higher protein concentration of available browse during the late dry-season rains.

Hunting and reproduction in quarry species.—Different prey can cope with human harvest according to their population dynamics and biological capacity (Cardillo et al. 2005), but their patterns of reproduction reflect their response to environmental and human disturbance. Predator–prey systems often co-evolve slowly through generations by the action of natural selection, with the appearance of phenotypical and behavioral traits in prey species that avoid their extinction (Kooijman and Lika 2014). However, the current reproductive strategies in wild species are not adapted to the typically more intensive levels of human predation, especially when hunting is directly impacting pregnant females and affecting the species' recruitment potential.

Water levels and hunting rates were shown to have a similar cyclical pattern over the period of 15 years for which data were available. Other studies in the Amazon basin have also demonstrated that hunters maximize their captures by taking into account seasonal water level changes (Kvist et al. 2001; Endo et al. 2016). This temporal convergence between heavier hunting and pregnancies in pacas is thus likely to adversely impact the species' population dynamics. A probable indication that hunting of pregnant paca females during high-water periods may affect populations of the species is available for the ASDR, where Valsecchi et al. (2014) demonstrated that paca hunting

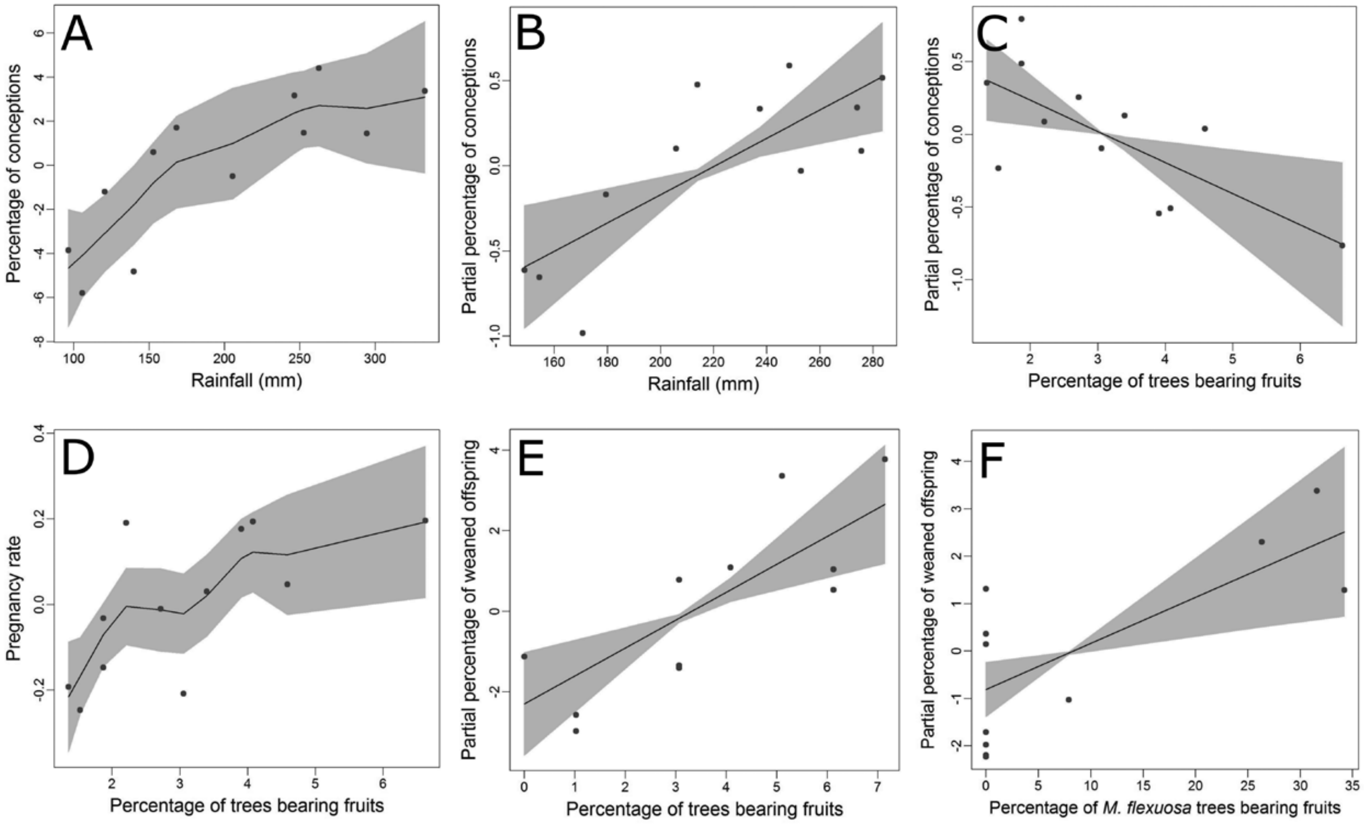

Fig. 6.—Relationship between (A) rainfall and the percentage of paca conceptions in the Amanã Sustainable Development Reserve, central Amazonia; (B) rainfall and percentage of paca conceptions in the Yavarí-Mirín River, western Amazonia; (C) percentage of trees bearing fruits in upland forest and percentage of paca conceptions in the Yavarí-Mirín River, western Amazonia; (D) percentage of trees bearing fruits in upland forest and pregnancy rate in the Yavarí-Mirín River, western Amazonia; (E) percentage of trees bearing fruits in swamp forest and percentage of weaned offspring, and (F) percentage of *Mauritia flexuosa* trees bearing fruits and percentage of weaned offspring in the Yavarí-Mirín River, western Amazonia. The gray area represents 95% *CI*s. Response variables are plotted on the y-axis in a scale of variation around the mean (μ = 0) calculated from the original data for models with a single predictor variable, and from partial residuals for models including more than 1 predictor variable.

is unsustainable and the species' abundance at this site significantly dropped over an 8-year period.

Management implications.—Pacas provide the largest proportion of wild meat consumed by local populations and even urban dwellers in the Amazon (Bodmer and Lozano 2001; Suárez et al. 2009; van Vliet et al. 2015). However, the species has a relatively low reproductive output, in which females only produce 1 young per pregnancy (Mayor et al. 2013b, 2017; El Bizri et al. 2017). The results presented here highlight the necessity for developing sustainable harvest strategies that are compatible with the target species' life history and their reproductive patterns. These strategies could include focusing hunting efforts on males or reducing hunting during the pregnancy season. However, avoiding hunting pacas during high water levels may not be possible for hunters. During the flooded period, fishing becomes difficult and hunting becomes the main source of meat supply during this period (Valsecchi et al. 2014; Endo et al. 2016), thus making it unlikely for a shift away from hunting pacas during the wet season. On the other hand, since male pacas can fertilize several females, hunting males exclusively during the high-water period, when pregnant females are more common, is feasible since rural Amazonian hunters pursue pacas by "spotlighting" (Valsecchi et al. 2014), thus permitting the identification of the sex of the animal and even the pregnancy stage of females (H. R. El Bizri, pers. obs.).

Another strategy to improve the state of hunted paca populations is to encourage the use of rotating hunting areas over the years or to protect areas during the hunting season that could act as refugia for females. This strategy would create a source–sink system where protected grounds would function as sources of individuals to repopulate areas depleted by hunting. This strategy has already been advocated as efficient to conserve species such as the culpeo fox (*Pseudalopex culpaeus*) in the Argentine Patagonia (Novaro et al. 2005) as well as ungulates in the Neotropics (Novaro et al. 2001; Naranjo and Bodmer 2007). A similar approach was effectively applied to recover giant Arapaima (*Arapaima gigas*) populations by encouraging community-based source–sink schemes; this system is now successfully applied throughout the Amazon (Campos-Silva et al. 2017). Here, we argue that source–sink systems could be equally applied for pacas. However, as all systems, these also need to be continuously monitored and adapted especially because the demand for paca meat is likely to increase in line with human population growth. Thus,

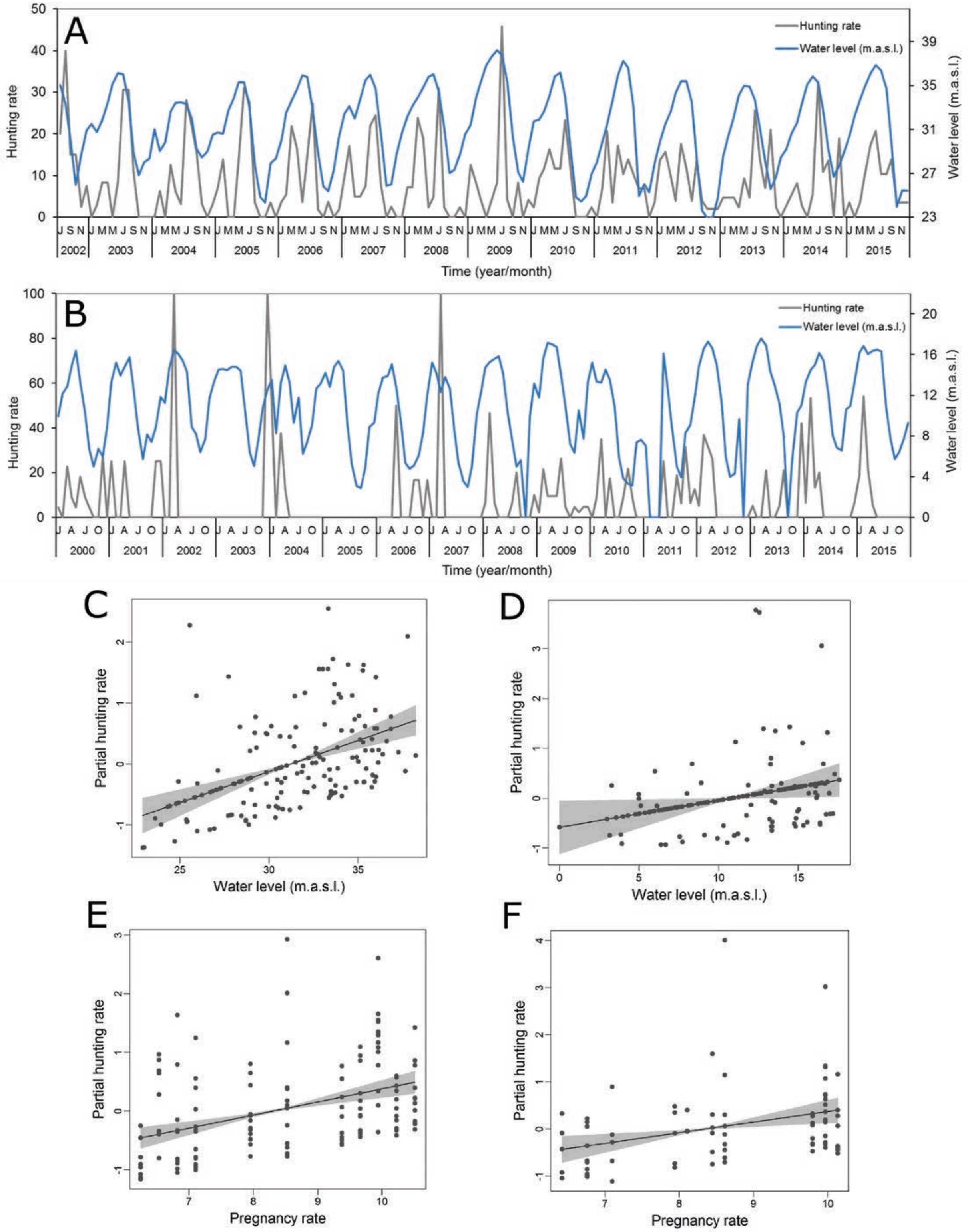

Fig. 7.—Temporal trends of the river water level and hunting rates (monthly percentage of harvested females within each year) in the (A) Amanã Sustainable Development Reserve and (B) Yavarí-Mirín River, in Amazonia. Relationship between river water level and hunting rates in the (C) Amanã Sustainable Development Reserve and (D) Yavarí-Mirín River, in Amazonia. Relationship between pregnancy rate and hunting rates in the (E) Amanã Sustainable Development Reserve and (F) Yavarí-Mirín River, in Amazonia. The gray area represents 95% *CI*s. Response variables are plotted on the y-axis in a scale of variation around the mean (μ = 0) calculated from partial residuals of the models.

additional measures such as setting quotas of the paca population that can be harvested per family, hunter, or community may be needed. Finally, since palm species are essential for pacas, and probably other Amazonian species, to achieve their highest reproductive potential, actions focused on conservation of swamp forest palm species, which are largely exploited by humans (Peters et al. 1989; Rull and Montoya 2014), are also critical.

Due to the fact that most hunting in Amazonia is determined by the annual variation in river water level, we argue that the impact we have observed in pacas could be mirrored in other species, and hence might affect the sustainability of wild meat, so vital for numerous inhabitants. Accordingly, strategies that ensure the sustainability of hunted Amazonian species must be based on reproductive information to minimize the impact on their populations when they are most vulnerable.

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