

Impact of prey availability and competitive interactions with hunters on the ocelot *Leopardus pardalis* (Linnaeus, 1758) population in Macanao Peninsula, Margarita Island, Venezuela

Impacto de la disponibilidad de presas e interacciones competitivas con cazadores en una población de cunagueros, *Leopardus pardalis* (Linnaeus, 1758), de la Península de Macanao, Isla de Margarita, Venezuela

María Abarca, Jon Paul Rodríguez, Margarita Lampo & Włodzimierz Jędrzejewski

Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Apdo. 20632, Caracas 1020-A, Venezuela.

Correspondencia: M. Abarca: mrabarca2@gmail.com

(Recibido: 02-02-2018 / Aceptado: 12-04-2018)

ABSTRACT

Carnivores strongly depend on prey populations due to their high metabolic rates and food demands, thus the spatial distribution of carnivores is often related to prey distribution. However, human impacts often reduce carnivore populations and limit their distribution. We studied the impact of prey distribution and hunting on the unique, isolated population of the ocelot *Leopardus pardalis* in the Macanao Peninsula of Margarita Island. By means of camera trapping and tracking we collected records of ocelots, rabbits *Sylvilagus floridanus* and partridges *Colinus cristatus* as well as records of hunting (mostly gun cartridges and traps set for rabbits and partridges) along 20 transects in various habitats, and we documented the activities of hunters. We developed a set of multiple regression models to analyse the relative impacts of prey and hunting on the number of ocelot records and compared these models with AICc (corrected Akaike Information Criterion). The best model included only two prey variables, records of rabbits and partridges, and predicted well the spatial distribution of ocelots ($R^2 = 0.56$). However, the second model ($R^2 = 0.62$) included the negative impact of hunting on ocelot distribution and got almost equal statistical support. We also found direct evidence of ocelots killed by hunters in retaliation for stealing prey from hunters' traps. We conclude that for the preservation of this unique island population of ocelots it is most important to ensure effective protection of the habitats that provide prey and to control hunting.

Keywords: carnivores, conservation, impact of hunting.

RESUMEN

Los carnívoros dependen directamente de las poblaciones de sus presas debido a sus altas tasas metabólicas y demanda de alimento, mientras que su distribución espacial a menudo se encuentra relacionada con la distribución de sus presas. Sin embargo, cada vez es más frecuente que el impacto humano reduzca las poblaciones de carnívoros, limitando así su distribución geográfica. Se estudió el impacto sobre la distribución de las presas y cacería sobre una población aislada de *Leopardus pardalis* en la Península de Macanao, Isla de Margarita, Venezuela. Por medio de fototrampeo y seguimiento, se obtuvieron registros de cunagueros, conejos (*Sylvilagus floridanus*) y perdices (*Colinus cristatus*), así como también indicios de cacería (registro de presencia de cazadores, cartuchos usados y trampas para conejos y perdices). Fueron analizadas 20 transectas en varios tipos de hábitats y se documentaron las actividades de distintos cazadores. Se desarrolló un modelo de regresión múltiple para analizar el impacto relativo sobre las presas y las actividades de cacería sobre el número de registros de felinos. Estos modelos se compararon usando una rutina estadística conocida como el Criterio de Información Akaike (AICc por sus siglas en inglés). El modelo más adecuado o ajustado solo usó dos variables de presas: registros de conejos y perdices.

El modelo seleccionado predijo bien la distribución espacial de los cunaguaros ($R^2 = 0.56$). Sin embargo, se encontraron evidencias de caza de cunaguaros, la cual es ejecutada por cazadores en retaliación hacia los felinos por robarles las presas de sus trampas. Se concluye que para la preservación de esta única población insular de cunaguaros es importante garantizar la protección efectiva de los hábitats que proporcionan las presas para estos felinos, así como el control de la cacería.

Palabras clave: carnívoros, conservación, impacto de cacería.

INTRODUCTION

The abundance and distribution of animal species is directly related to the availability and distribution of food resources (Krebs 2001). A relationship between food abundance and density and distribution of animals has been frequently documented for herbivores and carnivores. Carnivores strongly depend on their prey populations because of their high metabolic rates and high food demands (Carbone *et al.* 1999). However, human activities have marked effects on animal populations, and carnivores are usually the most affected (Purvis *et al.* 2000, Ceballos & Ehrlich, 2002). Various species of carnivores are declining worldwide, with hunting being one of the major drivers (e.g., Woodroffe 2000, Cardillo *et al.* 2004, Ripple *et al.* 2014, Jedrzejewski *et al.* 2017a, b). The reasons for hunting carnivores can vary between species and regions, but they are usually hunted for trophies, for the monetary value of their skins and fangs, or as retaliation if they kill domestic animals (Robinson & Bennett 2004, Henschel *et al.* 2011, Wilkie *et al.* 2011). Less often, carnivores are hunted for consumption of their meat (Jedrzejewski *et al.* 2017b).

Animal populations inhabiting islands are particularly vulnerable to human impacts. Because they are often isolated, migration cannot compensate for the mortalities caused by humans. The high vulnerability of island populations is a challenge for conservation. Good understanding of threats and factors that are causing population declines are very important for successful conservation actions (Purvis *et al.* 2000, Sanz 2007).

The geological history that has formed the Margarita Island has been reflected in its particular faunistic composition. Margarita and Trinidad are the only islands in the Caribbean with populations of native ocelot *Leopardus pardalis* (Meiri *et al.* 2004). The uniqueness of this island is also indicated by the occurrence of some endemic species, as the skunk *Conepatus semistriatus* and deer *Odocoileus margaritae* (Molina & Molinari 1999, Molinari 2007).

The main goal of this study was to investigate the relative importance of prey abundance and hunting on the spatial distribution of ocelots in the Macanao Peninsula of Margarita Island. Additionally, we wanted to investigate

how frequent the hunting is in Macanao in general, which species are hunted, what hunting methods are used and how they interfere with ocelot population, and what are the motivations to kill ocelots.

METHODS

The study area (100 km², from 10°57'54" N, 64°12'37" W to 11°2'36" N, 64°20'42" W) was located in the central part of Macanao, a 330 km² peninsula on the western part of Margarita Island, approximately 38 km north from the mainland Venezuelan coast in the Caribbean. Annual temperatures are above 25° C and annual rainfall varies between 125 and 500 mm. Most of Macanao has rough relief with various hills, canyons, and a mid-elevation mountain range (740 m) in the center. The vegetation is composed mostly of dry scrub, columnar cactus scrub, and tropical dry forests in the lower and middle elevations, and deciduous forests and a small patch of semi-cloudy forest at higher altitudes (Hoyos 1985, González *et al.* 2001, González 2007). The human population of Macanao is about 20,935 people (INE, 2014), distributed in 15 villages along the coast and one village in the mountains. Various human activities, particularly open-sky sand mining, have substantially modified the areas around the coast. For this reason, animal populations are confined to the central part of the Peninsula, where they take refuge in the mid and higher elevations (González *et al.* 2001, Sanz 2007). The "La Restinga" National Park protects some coastal areas in the north-east of Macanao.

Ocelots have been reported in Macanao, but not on the eastern part of Margarita Island (Bisbal 2001, Sánchez 2006). Among the potential prey species of the ocelot, the endemic subspecies of eastern cotton tail rabbit *Sylvilagus floridanus margaritae*, and the striped partridge *Colinus cristatus* (Emmons 1987, Ludlow and Sunquist 1987) are present in Macanao and also hunted for meat (Chapman & Flux 2008, Fergusson-Laguna 2008). The speckled spiny tree-rat (*Pattonomys semivillosus*) and various species of reptiles can supplement the ocelot's diet (Bisbal 1986, Ludlow & Sunquist 1987, Wang 2002).

We established 20 transects 0.6 to 3.6 km long (mean 2.0 km), usually along trails or streams and river beds. The

transects were located in the three main habitat types, proportionally to the share of these habitats in the study area: 1) forests (includes dry, semi-cloudy, riparian forest, 2) *cardonal* (includes columnar cacti scrub, grassland, cultivation and sandpits), and 3) dry scrub (Sanz 2004).

The study was conducted during two 23-day visits, in February and July, 2010. During each visit, we walked all the transects and recorded any signs of presence (visual observations, tracks, and feces) of ocelots and their main prey (rabbits and partridges). We also recorded the presence of hunters or any other evidence of hunting (cartridge remains or traps) (Bennett *et al.* 1940, Palomares *et al.* 2001). We also installed camera traps (Reconyx, Eco-tone, and Steelcamp) along the transects: 38 cameras in February and 31 in July. We attempted to distribute the cameras proportionally to the length of the transects, at similar distances between the cameras. However, because some cameras failed, we only obtained images from 30 cameras in February and 14 in July. The cameras worked 18 days on average. On the images, we counted records of ocelots, their prey (rabbits and partridges) as well as hunters. If an animal of the same species or a human was registered by a camera more than once during 30 minutes, we counted it as a single record (Kelly 2008, Kelly & Holub 2008).

For each transect we calculated indices of relative abundance of each species (ocelots, rabbits, and partridges) by combining all their records (tracks, groups of feces, visual observations, camera records) and dividing this number by

transect length. Similarly, we calculated hunting indices (number of cartridges or hunters observed during walks, and records of hunters by camera traps) and trapping indices (number of rabbit or partridge traps) (Rios-Uzeda *et al.* 2006, Monroy-Vilchis *et al.* 2008, Harmsen *et al.* 2010). In the further analysis we treated the number of ocelots per kilometer as a dependent variable and numbers of rabbits, partridges, records of gun hunting, and records of traps (each expressed in numbers per 1 km of transect) as independent (predictive) variables.

To explore which factors (those related with prey abundance or those with hunting) are associated with the spatial distribution of ocelots in Macanao, we calculated Pearson correlations between all variables. Also, we built a set of multiple regression models with all possible combinations of predictive variables and compared these models using the corrected Akaike Information Criterion (AICc) (Burnham & Anderson 2002). Additionally, we also inquired of hunters met in the field about cases of ocelot hunting and their motivations to hunt ocelots.

RESULTS

We obtained 46 records of ocelots, 273 of rabbits, and 38 of partridges. Records of hunters' activities were also common: we found 40 signs of hunting with guns (mostly cartridges but also photos of hunters from camera traps, Fig. 1). Additionally, we recorded 55 traps (53 set for rabbits and 2 for partridges) along the transects (Figs. 2a, b,



Figure 1. Hunters photographed by a camera trap in Chacaracual, Macanao Peninsula.



Figure 2. Common traps found along trails in the Macanao Peninsula. (a) Loop trap type “corralito” used to catch rabbits; (b) loop trap type “portillo” used to catch rabbits, (c-d) loop trap used for partridge – in the middle of the tray the hunter places water and the animal is caught when it passes through the only entrance to drink. The stealing of prey from these traps by ocelots can be also a reason for retaliatory killing of ocelots by hunters.

and c). Numbers of ocelot records were correlated with the number of rabbit or partridge records (Pearson $r = 0.52$ and 0.65 , respectively), but not with records of gun hunting or records of traps (Pearson $r = -0.06$ and 0.04 , respectively, Table 1).

The best multiple regression model, with the lowest AICc value, included only the prey variables (numbers of records of rabbits and partridges) ($R^2 = 0.56$, $SE = 0.66$, $p < 0.001$) (Table 2, 3). However, the second model that included gun hunting records, got only slightly lower support ($\Delta AICc = 0.49$, $R^2 = 0.62$, $SE = 0.63$, $p = 0.007$), al-

though the regression coefficient for hunting was not significantly different from zero in this model (Tables 2 and 3). During our field work, we also found direct evidences of ocelot hunting: a skull of a hunted ocelot in a hunter’s house and a hunter’s hide-out with hanging remains of a killed partridge, obviously as bait for ocelots, found in the forest. We also found one dead ocelot, with signs of being killed by a gunshot (Fig. 3). Additionally, three people encountered during field walks testified to ocelot hunting in Macanao. As the main motivation they declared retaliation to stealing hunters’ prey from traps by ocelots. They

Table 1. Pearson correlations between records of ocelots, rabbits, partridges, hunting with guns, and traps set by hunters (each N/km of transect), collected along our 20 transects in the Macanao Peninsula (Margarita Island) in February and July of 2010.

Variables	Ocelots	Rabbits	Partridges	Gun hunting	Traps
Ocelots	1.00				
Rabbits	0.52	1.00			
Partridges	0.65	0.25	1.00		
Gun hunting	-0.06	0.37	0.07	1.00	
Traps	0.04	0.14	-0.03	0.44	1.00

Table 2. Comparison of multiple linear regression models predicting number of ocelot records on 20 transects in Macanao Peninsula. Dependent and predictive variables expressed as N records/km of transect. AICc denotes the corrected Akaike Information Criterion (see Methods).

Model No	Predictive variables in the model	AICc	Δ AICc	AICc weighth
1	Rabbits, Partridges	47.31	0	0.40
2	Rabbits, Partridges, Gun hunting	47.8	0.49	0.31
3	Partridges	49.59	2.28	0.13
4	Rabbits, Partridges, Traps	50.93	3.62	0.06
5	Rabbits, Partridges, Gun hunting, Traps	51.21	3.9	0.06
6	Partridges, Gun hunting	52.41	5.1	0.03
7	Rabbits	54.05	6.74	0.01

Table 3. Parameters of the two best-fitting multiple regression models of numbers of ocelot records on 20 transects in Macanao Peninsula in 2010.

Effect	Coefficient	Standard Error	t	p-Value
A. Top model, Δ AICc = 0				
Constant	0.523	0.20	2.64	0.017
Rabbits	0.051	0.02	2.31	0.034
Partridges	0.209	0.06	3.30	0.004
B. Second model, Δ AICc = 0.49				
Constant	0.607	0.20	3.10	0.007
Rabbits	0.064	0.022	2.85	0.012
Partridges	0.206	0.060	3.41	0.004
Gun hunting	-0.194	0.118	-1.65	0.119

also testified to consuming ocelot meat and occasional selling ocelot skins in Macanao.

DISCUSSION

The close relationship between the abundance of ocelots and number of rabbits and partridges indicates that ocelots probably often consume these prey species in Macanao, al-

though there have been no direct studies on ocelot food preferences on this island. Other carnivore studies have also shown strong correlations between the distribution of carnivores and their prey (e.g. Jędrzejewska & Jędrzejewski 1998, Palomares *et al.* 2001, Karanth *et al.* 2004). This suggests that persistence of the ocelot population in Macanao is strongly dependent on the effective protection of habitats important for rabbits and partridges.



Figure 3. Photo of an ocelot killed by hunters, found during the field work, Boca Chica, Macanao Peninsula.

Hunting appears to be frequent and widespread in Macanao and includes hunting with guns and trapping. Importance of hunting for the ocelot population was confirmed by our modeling as well as by the direct evidences of killed ocelots and interviews with hunters. Our models indicate that hunting can influence ocelot distribution and possibly ocelot numbers in certain habitats. The main reason to kill ocelots appears retaliation to stealing hunters' prey from traps. Other studies demonstrated that hunting can pose a real danger for carnivore populations, often being one of the main causes of their extirpations (e.g. Ceballos & Ehrlich 2002, Wilkie *et al.* 2011). Retaliatory killing induced by conflicts between humans and carnivores can be especially effective in reducing or eliminating carnivore populations (Jędrzejewski *et al.* 2017b). Taking into account that the population of ocelots in Macanao is isolated and must be very small because of the small area of the island – any increase of hunting could pose a real threat for further persistence of ocelots on Margarita Island.

We conclude that for the preservation of this unique island population of ocelots it is most important to ensure an effective protection of habitats that provide prey for ocelots and to control hunting.

ACKNOWLEDGEMENTS

This study was funded by the Instituto Venezolano de Investigaciones Científicas (IVIC), Idea Wild (2007),

Latin American Student Fellowship from American Society of Mammalogists (2007), and the Iniciativa de Especies Amenazadas-PROVITA (2007-2008, 2010-2011). We are grateful to José Manuel Briceño-Linares and Pablo A. Millán from PROVITA in Macanao for their logistic support during the field work. We are also grateful to María de Lourdes González (Malú), Romauro Vásquez y Gonzalo Medina for their help during field work. We would like to thank Enrique González from IVIC's Department of Scientific Photography for his help with the processing of photos. We thank Grisel Velásquez and Sergio Zambrano for their help with preparing the maps for the field work.

REFERENCES

- Bennett, L. J., P. F. English & R. McCain. 1940. A study of deer populations by use of pellet-group counts. *The Journal of Wildlife Management* 4: 398–403.
- Bisbal, F. J. 1986. Food-habits of some Neotropical carnivores in Venezuela (Mammalia, Carnivora). *Mammalia* 50: 329–339.
- Bisbal, F. J. 2001. *Vertebrados terrestres del Estado Nueva Esparta*. Maracay: Ministerio del Ambiente y los Recursos Naturales.
- Burnham, K P & D. R. Anderson. 2003. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media
- Carbone, C., G. M. Mace, S. C. Roberts & D. W. Macdonald. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature* 402: 286–288.

- Cardillo, M., A. Purvis, J. Bielby, G. M. Mace, W. Sechrest & J. L. Gittleman. 2004. Human population density and extinction risk in the world's carnivores. *PLoS Biol* 2: e197.
- Ceballos, G. & P. R. Ehrlich. 2002. Mammal population losses and the extinction crisis. *Science* 296: 904–907.
- Chapman, J. A. & J. E. C. Flux. 2008. Introduction to the Lagomorpha. In: Alves P. C., N. Ferrand & K. Hackländer (eds.): *Lagomorph biology*: Berlin / Heidelberg: Springer.
- Emmons, L. H. 1987. Comparative feeding ecology of felids in a Neotropical rain-forest. *Behavioral Ecology and Sociobiology* 20: 271–283.
- Fergusson-Laguna, A. 2008. El aprovechamiento sustentable de la diversidad biológica en Venezuela. Pp.: 185–204. In: Machado-Allison A. (ed.): *Simposio Investigación y Manejo de Fauna Silvestre en Venezuela en homenaje al Dr. Juhani Ojasti*. Caracas: Academia de Ciencias Físicas, Matemáticas y Naturales.
- González, L. A., A. Prieto & P. Cornejo. 2001. Estado actual de los mamíferos terrestres en la Isla de Margarita, Venezuela. *Saber* 13: 87–96.
- González, V. 2007. La vegetación de la Isla de Margarita y sus interrelaciones con el ambiente físico. *Memoria de la Fundación La Salle de Ciencias Naturales* 167: 131–161.
- Harmsen, B. J., R. J. Foster, S. Silver, L. Ostro & C. P. Doncaster. 2010. Differential use of trails by forest mammals and the implications for camera-trap studies: a case study from Belize. *Biotropica* 42: 126–133.
- Henschel, P., L. T. B. Hunter, L. Coad, K. A. Abernethy & M. Mühlenberg. 2011. Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bush meat hunters. *Journal of Zoology* 285: 11–20.
- Hoyos-F., J. 1985. *Flora de la isla Margarita, Venezuela*. Caracas: Sociedad y Fundación La Salle de Ciencias Naturales. Editorial Texto.
- Instituto Nacional Estadística. República Bolivariana de Venezuela. 2014. *XIV Censo nacional de población y vivienda. Resultados por Entidad Federal y Municipio del Estado Nueva Esparta*. 95 pp.
- Jeźdrzejewska, B. & W. Jeźdrzejewski. 1998. *Predation in vertebrate communities: the Białowieża Primeval Forest as a case study*. Ecological Studies 135. Germany: Springer-Verlag Berlin Heidelberg.
- Jeźdrzejewski, W., E. O. Boede, M. Abarca, A. Sánchez-Mercado, J. R. Ferrer-Paris, M. Lampo, G. Velásquez, R. Carreño, Á. L. Viloria, R. Hoogesteijn, H. S. Robinson, I. Stachowicz, H. Cerda, M. del Mar Weisz, T. R. Barros, G. A. Rivas, G. Borges, J. Molinari, D. Lew, H. Takiff & K. Schmidt. 2017a. Predicting carnivore distribution and extirpation rate based on human impacts and productivity factors; assessment of the state of jaguar (*Panthera onca*) in Venezuela. *Biological Conservation* 206: 132–142.
- Jeźdrzejewski, W., R. Carreño, A. Sánchez-Mercado, K. Schmidt, M. Abarca, H. S. Robinson, E. O. Boede, R. Hoogesteijn, Á. L. Viloria, H. Cerda, G. Velásquez & S. Zambrano-Martínez. 2017b. Human-jaguar conflicts and the relative importance of retaliatory killing and hunting for jaguar (*Panthera onca*) populations in Venezuela. *Biological Conservation* 209: 524–532.
- Karanth, K. U., N. S. Kumar, J. D. Nichols, W. A. Link & J. E. Hines. 2004. Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America* 101: 4854–4858.
- Kelly, M. J. 2008. Design, evaluate, refine: camera trap studies for elusive species. *Animal Conservation* 11: 182–184.
- Kelly, M. J. & E. L. Holub. 2008. Camera trapping of carnivores: trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. *Northeastern Naturalist* 15: 249–262.
- Krebs, C. J. 2001. *Ecology. The experimental analysis of distribution and abundance*. San Francisco: Benjamin Cummings-Addison Wesley Longman Inc.
- Ludlow, M. E. & M. E. Sunquist. 1987. Ecology and behavior of ocelots in Venezuela. *National Geographic Research* 3: 447–461.
- Meiri, S., T. Dayan & D. Simberloff. 2004. Body size of insular carnivores: little support for the island rule. *The American Naturalist* 163: 469–479.
- Molina, M. & J. Molinari. 1999. Taxonomy of Venezuelan white-tailed deer (*Odocoileus*, Cervidae, Mammalia), based on cranial and mandibular traits. *Canadian Journal of Zoology* 7: 632–645.
- Molinari, J. 2007. Variación geográfica en los venados de cola blanca (Cervidae, *Odocoileus*) de Venezuela, con énfasis en *O. margaritae*, la especie enana de la Isla de Margarita. *Memoria de la Fundación la Salle de Ciencias Naturales* 167: 29–72.
- Monroy-Vilchis, O., O. Sánchez, U. Aguilera-Reyes, P. Suárez & V. Urios. 2008. Jaguar (*Panthera onca*) in the State of Mexico. *The Southwestern Naturalist* 53: 533–537.
- Palomares, F., M. Delibes, E. Revilla, J. Calzada & J. M. Fedriani. 2001. Spatial ecology of Iberian lynx and abundance of European rabbits in southwestern Spain. *Wildlife Monographs* 148: 1–36.
- Purvis, A., J. L. Gittleman, G. Cowlishaw & G. M. Mace. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 267: 1947–1952.
- Rios-Uzeda, B., H. Gómez & R. B. Wallace. 2006. Habitat preferences of the Andean bear (*Tremarctos ornatus*) in the Bolivian Andes. *Journal of Zoology* 268: 271–278.
- Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic & M. P. Nelson. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343: 1241484.
- Robinson, J. G. & E. L. Bennett. 2004. Having your wildlife and eating it too: an analysis of hunting sustainability across tropical ecosystems. Pp.: 397–408. In: *Animal Conservation Forum*. Cambridge University Press.
- Sánchez, J. 2006. *Inventario de fauna de la Península de Macanao, Estado Nueva Esparta. Serie Informes Técnicos ONDB/*

- IT/424. Maracay: Ministerio del Ambiente. Viceministerio de Conservación Ambiental. Oficina Nacional de Diversidad Biológica. Centro Nacional de Conservación de Recursos Genéticos. Museo de la Estación Biológica de Rancho Grande, 22 pp.
- Sanz, V. 2004. Ecología de *Amazona barbadensis* (Aves: Psittacidae). Caracterización y uso de hábitat en la Península de Macanao (Isla de Margarita) a diferentes escalas espaciales y temporales. Caracas: Universidad Central de Venezuela.
- Sanz, V. 2007. ¿Son las áreas protegidas de la Isla de Margarita suficientes para mantener su biodiversidad? Análisis espacial del estado de conservación de sus vertebrados amenazados. *Memoria de la Fundación La Salle de Ciencias Naturales* 167: 111–130.
- Wang, E. 2002. Diets of ocelots (*Leopardus pardalis*), margays (*L. wiedii*), and oncillas (*L. tigrinus*) in the Atlantic Rainforest in southeast Brazil. *Studies on Neotropical Fauna and Environment* 37: 207–212.
- Wilkie, D. S., E. L. Bennett, C. A. Peres & A. A. Cunningham. 2011. The empty forest revisited. *Annals of the New York Academy of Sciences* 1223: 120–128.
- Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* 3: 165–173.