Conservation Biology

Contributed Paper

Using spatial patterns in illegal wildlife uses to reveal connections between subsistence hunting and trade

Ada Sánchez-Mercado,* ¶ Marianne Asmüssen,† Kathryn M. Rodríguez-Clark,† Jon Paul Rodríguez,† and Wlodzimierz Jedrzejewski†

*Centro de Estudios Botánicos y Agroforestales, Instituto Venezolano de Investigaciones Científicas (IVIC), P.O. Box 20632, Caracas, 1020-A, Venezuela

†Centro de Ecología, Instituto Venezolano de Investigaciones Científicas (IVIC), P.O. Box 20632, Caracas, 1020-A, Venezuela

Abstract: *Although most often considered independently, subsistence hunting, domestic trade, and international trade as components of illegal wildlife use (IWU) may be spatially correlated. Understanding how and where subsistence and commercial uses may co-occur has important implications for the design and implementation of effective conservation actions. We analyzed patterns in the joint geographical distribution of illegal commercial and subsistence use of multiple wildlife species in Venezuela and evaluated whether available data were sufficient to provide accurate estimates of the magnitude, scope, and detectability of IWU. We compiled records of illegal subsistence hunting and trade from several sources and fitted a random-forest classification model to predict the spatial distribution of IWUs. From 1969 to 2014, 404 species and 8,340,921 specimens were involved in IWU, for a mean extraction rate of 185,354 individuals/year. Birds were the most speciose group involved (248 spp.), but reptiles had the highest extraction rates (126,414 individuals/year vs. 3,133 individuals/year for birds). Eighty-eight percent of international trade records spatially overlapped with domestic trade, especially in the north and along the coast but also in western inland areas. The distribution of domestic trade was broadly distributed along roads, suggesting that domestic trade does not depend on large markets in cities. Seventeen percent of domestic trade records overlapped with subsistence hunting, but the spatial distribution of this overlap covered a much larger area than between commercial uses. Domestic trade seems to respond to demand from rural more than urban communities. Our approach will be useful for understanding how IWU works at national scales in other parts of the world.*

Keywords: poaching, random forest, subsistence hunting, Venezuela, wildlife illegal trade

Aplicación de Patrones Espaciales en los Usos Ilegales de la Vida Silvestre para Revelar las Conexiones entre la Caza de Subsistencia y el Comercio

Resumen: *Aunque muchas veces son considerados independientemente, la caza de subsistencia y el comercio doméstico e internacional como componentes del uso ilegal de vida silvestre (UIVS) pueden estar correlacionados espacialmente. Entender cómo y dónde los usos comerciales y de subsistencia pueden co-ocurrir tiene implicaciones importantes para el diseño y la implementación de acciones efectivas de conservación. Analizamos los patrones en la distribución geográfica conjunta del uso ilegal comercial o por subsistencia de múltiples especies de vida silvestre en Venezuela y evaluamos si los datos disponibles eran suficientes para proporcionar estimaciones correctas de la magnitud, el alcance y la detectabilidad del UIVS. Compilamos los registros del comercio y la caza de subsistencia ilegales de varias fuentes y acoplamos un modelo de bosques aleatorios para predecir la distribución espacial del UIVS. De 1969 a 2014, 404 especies y 8,340,921 especímenes estuvieron involucrados en UIVS, para una tasa de extracción media de 185,354 individuos/año. Las aves fueron el grupo involucrado más rico en especies (248 spp.), pero los reptiles tuvieron las tasas de extracción más altas (126, 414 individuos/año contra 3,133 individuos/año para las aves). El 88% de los registros del comercio internacional se solapó espacialmente con el comercio doméstico, especialmente en el norte y a lo largo de la costa, pero también en las áreas occidentales tierra adentro. La extensión del comercio doméstico estuvo distribuida ampliamente a lo largo de las carreteras, lo que sugiere que el comercio doméstico*

¶*email asanchez@ivic.gob.ve*
Paper submitted December 11, 2015; revised manuscript accepted April 16, 2016.

DOI: 10.1111/cobi.12744

no depende de un gran mercado en las ciudades. El 17% de los registros de comercio doméstico se solapó con la caza por subsistencia, pero la distribución espacial de este solapamiento cubrió un área mucho mayor que entre los usos comerciales. El comercio doméstico parece responder a la demanda rural más que a la demanda de las comunidades urbanas. Nuestra estrategia será útil para entender cómo funcionan los UIVS a escala nacional en otras partes del mundo.

Palabras Clave: bosques aleatorios, caza furtiva, caza por subsistencia, mercado ilegal de vida silvestre, Venezuela

Introduction

Illegal wildlife use (IWU), any use of nondomesticated fauna that violates national or international regulations, is a major threat to biodiversity globally and can have far-reaching impacts on livelihoods and human food security (Broad et al. 2003; Gavin et al. 2010). Tropical countries in particular may experience chronic and intense IWU when biodiversity levels are high and law enforcement is weak. Illegal international trade in wildlife has perhaps received the most attention, has a value of approximately \$7–10 billion/year, and affects thousands of species worldwide (Lawson & Vines 2014). However, such estimates exclude illegal domestic trade and subsistence hunting. Although poorly documented, the high value of domestic trade (approximately \$175 million/year in the Amazon basin [Nasi et al. 2008] and \$24–205 million across West and Central Africa [Gandiwa et al. 2013]) has large negative effects on biodiversity. Domestic trade is frequently motivated by social, cultural, and economic factors (Nasi et al. 2008). Conversely, subsistence hunting has been seen typically as a low-impact activity practiced mostly by indigenous communities motivated by food insecurity, protection against crop raiding, or tradition (MFunda & Røskaft 2010).

Legislation and conservation actions in tropical countries are based on the hypothesis that in different areas wildlife uses occur independently of one another. For example, some countries have suspended importation of some endangered species (Di Minin et al. 2015) under the assumption that commercial trade is higher within cities and coastal areas, where population and economic infrastructures are denser than in the interior and where access to markets is higher (Maingi et al. 2012). Other countries recognize subsistence hunting as a legitimate form of wildlife use, and local communities are constrained by license systems that include seasons, bag limits, and lists of species and age classes that can be taken (Ntiamoa-Baidu 1997). The implementation of these controls makes sense because subsistence hunting is assumed to occur principally clustered around rural communities, closer to areas where resource availability is higher. However, subsistence hunting and commercial trade (domestic and international) may be spatially correlated (i.e., similar uses occur in nearby localities). Subsistence hunting can blur into domestic trade for rural peoples where wildlife supplements diet and income and generate a "bushmeat crisis" (Nasi et al. 2008). Similarly, there is a well-documented association between domestic and international trade in wildlife pets and medicinal derivatives (Santos et al. 2011).

Understanding how and where subsistence and commercial uses may co-occur has important implications for the design and implementation of effective conservation actions such as law enforcement and environmental education. Evaluating how different illegal activities may be spatially interrelated is not a simple task. First, illegal traders and hunters may be strongly motivated to conceal their activities, making data collection difficult (Knapp et al. 2010). Second, many countries lack reliable mechanisms to systematically compile wildlife-use records, legal or otherwise (Dongol 2012; Challender et al. 2015), and most data are in the grey literature. Records of IWU are usually opportunistically collected and have substantial geographic and temporal biases (Golden et al. 2013). A promising recent approach to deal with these data-collection challenges involves fitting spatially explicit models to evaluate the relative role of anthropogenic and ecological factors in determining the geographical distribution of IWUs (Maingi et al. 2012; Ziegler et al. 2016). Although the incorporation of spatial dimension makes these studies innovative, most focus on only a single species, even though most hunters and traders deal with multiple species (Conteh et al. 2015), and one use (e.g., subsistence hunting or international trade). A single-species focus ignores important correlations across taxa and limits understanding of the scope and magnitude of impacts. Although some hypothesize generally that uses may be interrelated (e.g., de Merode et al. 2004; Nasi et al. 2008; Lindsey et al. 2013), none have attempted the rigorous analyses required to test the prediction of joint spatial patterns in IWU.

To overcome these limitations and test this prediction, we analyzed patterns in the geographical distribution of illegal commercial and subsistence use of multiple wildlife species with data from Venezuela. In contrast to standard assumptions of independence among IWUs, we hypothesized that domestic trade co-occurs spatially to a large extent (but in different areas) with international trade and subsistence hunting. We also aimed to evaluate whether available data were sufficient to provide accurate estimates of the magnitude, scope, and detectability of IWU across Venezuela over time. To do this, we compiled records of illegal hunting and trade from

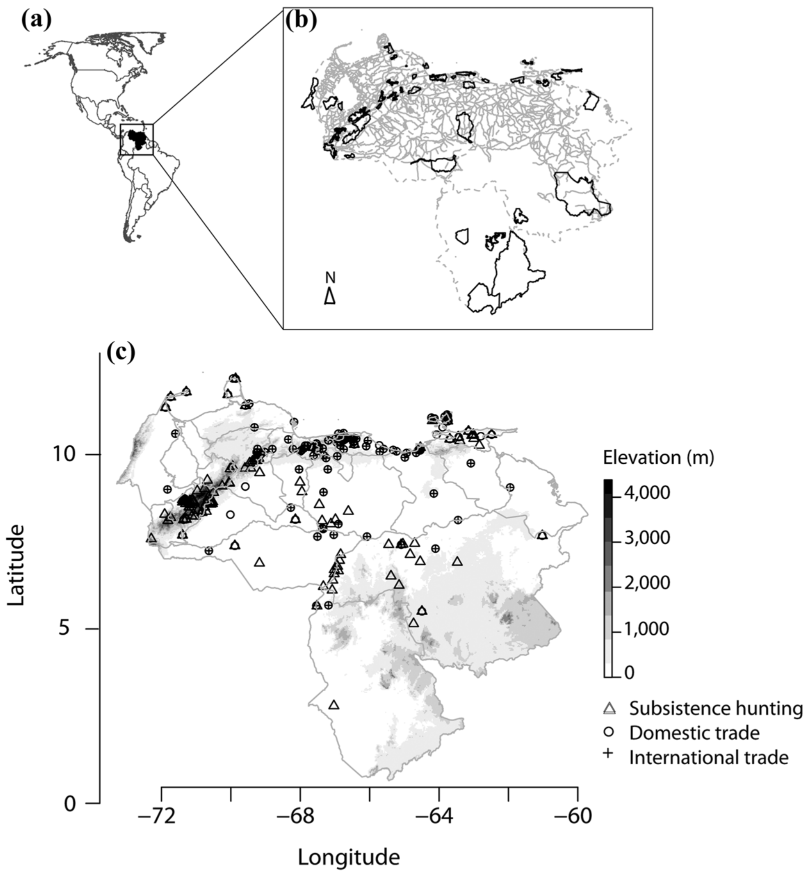

Figure 1. (a) Relative location of Venezuela in South America, (b) major geographical features in the study area (dotted lines, political divisions; solid grey lines, primary roads; black lines, protected areas), and (c) elevation and illegal wildlife use records by use.

sources that varied in quality and quantity of information. We evaluated temporal and geographical biases and then used this information to fit a random-forest (RF) classification model (Cutler et al. 2007) to characterize spatial interactions among IWUs based on their association with anthropogenic and ecological factors. Random forest is particularly useful for supervised classifications when the response is a categorical variable with >2 possible values. Although commonly applied in species-distribution models and remote-sensing classification, to our knowledge this is the first time RF has been used to evaluate IWU patterns (Franklin 2010).

We used data from Venezuela because the country is tropical and megadiverse, has a deep tradition of commercial and subsistence wildlife use (Ojasti 1993), and lacks a national infrastructure for wildlife-use assessment and law enforcement (Kaufmann et al. 2011). This combination of factors is not uncommon, so an approach that works with Venezuelan data is likely to be broadly applicable.

Methods

Study Area and Legal Framework

Venezuela is among the most urban of South American countries; most of its approximately 30 million inhabitants (Instituto Nacional de Estadística 2010) live in cities along the coast (Figs. 1a & b). Large-scale habitat conversion has occurred north of the Orinoco River, whereas the southern half of the country has retained much of its precolonial vegetation (Rodríguez et al. 2010).

Wildlife administration is under the Ministry for Ecosocialism and Waters (previously Ministry for the Environment), but law enforcement falls under the military and police; the administrative agency plays a supporting role (Ojasti 1993). Venezuelan legislation permits wildlife use via special licenses, including for scientific sampling (including eggs and juveniles), pest control, sport, and commercial hunting. Subsistence hunting is not recognized as separate from sport hunting. Wildlife take without a permit is punishable by fines and up to 2 years in prison; possession is penalized by seizure of the animal (Congreso de la República de Venezuela 1970; República de Venezuela 2012). Venezuela ratified CITES in 1977 and restricts exports of all native wildlife except for the products of captive breeding or those deriving from government-sanctioned management plans, such as capybara (*Hydrochaeris hydrochaerus*) and caiman (*Caiman crocodrilus*). We defined as illegal all take without permits of undomesticated terrestrial birds, reptiles, amphibians, and mammals from protected or private areas and uses exceeding established limits or seasons. This included unlicensed harvest of eggs or juveniles and domestic or international trade of live specimens.

IWU Classification and Data Sources

We classified records by use type into 3 nonexclusive categories: subsistence hunting, the direct harvest of entire specimens or their parts (meat, bones, eggs, etc.) for consumption, traditional medicine, or other uses excluding barter or sale regardless of type of hunter or hunting method; domestic trade, whole specimens or their parts offered for sale or barter to local buyers either directly by hunters or by intermediate dealers who obtained items from hunters or other local intermediates; and international trade, similar to domestic trade but with sales by hunters or intermediates to buyers abroad.

Using these definitions, we compiled 4486 records of subsistence hunting, domestic trade, and international trade with data from enforcement agencies, the CITES trade database, and published and unpublished literature. We used data from 2 types of enforcement agencies: the Venezuelan environmental ministry (VEM) and the U.S. Fish and Wildlife Service (USFWS). Data from the VEM were compiled by Asmussen-Soto (2010) and consisted of 1042 records digitized from reports of seized wildlife at the national level from 1990 to 2000. For 2001–2009, only reports from 3 regional offices (Distrito Capital, Aragua, and Cojedes states) were available. Personnel from VEM strongly argued that in all cases their reports refer to national traders selling goods on international markets and that the final destination of specimens depended on the effectiveness and speed of response of international dealers. If international dealers delay their responses, then national traders try to sell goods on domestic markets before specimens sicken or die (A. Martínez, personal communication). Thus, we classified VEM's records as domestic and international trade to avoid underestimating international trade when the trade was detected at the national level. Data from USFWS on all illegal shipments entering the United States from Venezuela from May 1993 to September 1998 (333 records) was compiled by Rodriguez (2000). We searched the CITES trade database (CITES 2009) for Venezuelan records from 1975 to 2015. We obtained 1808 records of specimens and items seized from Venezuela.

To search the published literature, we used 5 online databases (ISI Web of Knowledge, Scirus, JSTOR, Google Scholar, and Zoological Records). We focused on ecology, conservation, and anthropology journals and used keywords in English and Spanish related to wildlife use: *Venezuela*, *poach*, *hunt*, *harvest*, *consumption*, *trade*, and *traffic*. We also consulted 2 related web pages: The Stage of the World's Sea Turtles (SWOT 2003) and TRAFFIC (2008). To improve detection in grey literature, we requested support from Red Ara Venezuela (http://red-ara-venezuela.blogspot.com/), a network of Venezuelan environmental nongovernmental organizations, and asked wildlife managers and researchers we knew for information and additional contacts who may have information about wildlife trade. This search yielded 58 documents containing 1303 IWU records (Fig. 1c & Supporting Information).

We considered each record (i.e., a row in our database) as a single observation in time of a unique combination of the following: species involved, observation date, location, resource extracted (specimen or part), quantity reported (number of specimens or eggs or kilograms of meat or parts), and reported use (domestic trade, international trade, subsistence). Our database included all uses described for a given report. If more than one use was described, each use was included in the same row. Thus, the structure of the database was based on species, which allowed us to quantify the amount of IWU by taxonomic class and source and to visualize temporal patterns.

For records without specific geographic coordinates, we used the description of the location (place names, geographic features, etc.) to assign latitude and longitude based on gazetteers (i.e., directory of georeferenced localities; GIS Data Depo, DIVA GIS). When different coordinates were provided by each gazetteer, we calculated the mean value and error of latitude and longitude. If the error was bigger than the cell resolution used to project our predictions (1 km^2), we discarded the record. We used Encyclopedia of Life (www.eol.org) validate common and scientific names (considering synonyms, alternative spellings, and subspecies).

Scope and Magnitude of IWU

To visualize temporal variation in IWU sampling effort, we plotted the proportion of records corresponding to each use type by year. Records were collected opportunistically by state agencies or researchers using direct observations or secondhand reports. Thus, data were available only where and when nonrandom patrols and research occurred and only for species of interest. Because of these spatial, temporal, and taxonomic biases, truly accurate estimates of the magnitude and scope of IWU are not possible (Gavin et al. 2010). However, we were able to summarize the number of species and specimens recorded, by taxonomic class, and calculate a biased extraction rate as the yearly average of this number across the period considered. We also summarized the number of records obtained from each source according to type of use to evaluate the complementarity among sources.

Co-Occurrence of Subsistence and Commercial IWUs

We evaluated relationships among IWUs by fitting a classification model. We used only the 1929 georeferenced records (i.e., spatial dataset) from 1990 or later because most of our predictive variables were built with data from this date or later.

We restructured the spatial data set so that is was based on use type not species. For that, we split records with multiple uses and added a row for every use; information in other columns did not change (locality, species, etc.). This artificially increased the data set (from 1929 georeferenced records to 4219 records) with identical geographic and temporal information. We did this to obtain a response variable for our model—use type—and to retain geographic information and information on multiple-use status for error analyses evaluating use overlap.

For our spatial models, we used RF to predict spatial patterns of wildlife use type. Although regression models are used to predict spatial patterns in IWU by estimating the probability of occurrence of a single use type, their requirement of a single dependent variable make them inappropriate for understanding the simultaneous occurrence of multiple uses. Classification methods such as RF allow a dependent variable with more than 2 categories or classes and are better able to reveal the contribution and behavior of multiple independent variables, whose effects may be otherwise lost in regression models (Liaw & Wiener 2002).

We implemented RF in the randomForest package in R (Liaw & Wiener 2002). We built each classification tree with a training data set containing 60% of records sampled randomly with replacement from the original data and containing a random subset of predictor variables selected from the full set of predictor variables (Breiman 2001). We resampled records to create 500 classification trees in our RF.

We considered 8 continuous and one categorical predictor variable (Table 1). Direct, reliable measures of household purchasing power were not available, so we used a combination of livestock density, land cover, and aridity index as indicators of agricultural production, which we in turn used as a measure of average household wealth. We assumed that areas with relatively more agricultural and arid areas were on average more rural and poorer (Machado-Allison 2005). We evaluated the relative importance of predictor variables with the Gini index of variable importance values (GIVI), defined as the averaged Gini decrease in node impurities over all trees in the forest (Breiman 2001).

Model Evaluation

We validated the prediction of each tree in the RF with the remaining 40% of records (i.e., out-of-bag observations [OOB]). An estimate of the misclassification error rate was calculated for each OOB observation and averaged over all trees in the forest (Cutler et al. 2007).

Our classification errors measured 2 sources of error: misclassification and overlapping. Overlap occurs when records from different classes have very similar or identical characteristics (i.e., values of predictive variables) that make it difficult or impossible to assign the overlapped record to any class (Denil & Trappenberg 2010).

To discriminate between overlap (the process of interest) and misclassification (true error), we fitted an RF model with all records, estimated OOB classification error, and used in-bag observations to calculate an analogous in-bag error. If the model misclassified in-bag observations, given that these were used to build the trees, then we could attribute this classification error to overlap. The difference between OOB error and in-bag error therefore estimated the misclassification error of the model.

We visualized the spatial pattern of predictions for each IWU category with the predict function of the randomForest package (Liaw & Wiener 2002) and a raster stack of predictive variables at a resolution of 1 km^2. We also visualized the spatial distribution of overlapping uses by multiplying the respective estimates of probability for each IWU category.

Results

Scope and Magnitude of IWU

The records we found spanned 45 years (1969–2014) and revealed 404 species (online Supporting Information) and 8,340,921 specimens involved in IWU. Average extraction rate was 185,354 specimens/year (Table 2). Birds were the most speciose group involved in IWU (248 spp.), and most bird records involved domestic and international trade. Mammal records involved 93 spp., and although a similar number of records were detected for all uses, more species were used for domestic trade and subsistence hunting. Reptiles (58 spp.) were used mainly for international trade but had the highest extraction rates in terms of numbers of individuals (average 126,414 individuals/species and 174,572 individuals/year) (Table 2).

International trade was the most frequently reported use (3238 records), followed by domestic trade (1577 reports). We obtained 984 records of subsistence hunting. Sources of records were complementary rather than overlapping with respect to use type. The VEM, USWFS, and CITES sources contributed 98% of international trade records (3183 records) and 66% of domestic trade records (1042 records of 1577), whereas grey and published literature provided all records for subsistence hunting.

Temporal and Spatial Biases in IWU

In general, the rate of accumulation of IWU records increased over time (Fig. 2a). The proportion of records associated with each wildlife use varied before 1990, but subsequently the proportion of reports in each use category was roughly constant (Fig. 2b). From 1968 to 1990 the amount of international and domestic trade increased

Table 1. Independent variables used to fit the random-forest model of illegal wildlife use.

Variable	Source	Original resolution (decimal degree)	Type	Description
Distance to road	CGIAR Institute 2010	0.0274	continuous	raster derivate from a shape file retrieve from the GIS Unit of Ecology Centre at Instituto Venezolano de Investigaciones Científicas; distance in meters calculated using distance function from Raster package in R; rinal resolution 2.7 km
Distance to protected area	CGIAR Institute 2010	0.0274	continuous	raster derivate from a shape file retrieve from the GIS Unit of Ecology Centre at Instituto Venezolano de Investigaciones Científicas; distance calculated in meters using distance function from Raster package in R; final resolution 2.7 km
Forest cover	DiMiceli et al. 2011	0.008	continuous	raster derivate from all 7 bands of the Moderate-resolution Imaging Spectroradiometer (MODIS) sensor; value range 0–100% of pixel area covered by woody vegetation
Land cover	CGIAR Institute 2010	0.008	categorical	raster based on AVHRR satellites acquired between 1981 and 1994; analyzed to distinguish 22 land-cover classes from tree forest, mosaic, cultivated, and managed areas
Aridity index	Trabucco & Zomer 2009	0.008	continuous	data set provides raster climate data related to evapotranspiration processes and rainfall deficit for potential vegetative growth
Human population density	Center for International Earth Science Information Network 2000	0.004	continuous	raster that renders global population data; population estimates for 1990, 1995, and projected to 2000
Livestock density	Ministerio del Poder Popular de Agricultura y Tierra 2010	0.017	continuous	raster based on the number of livestock in x km^2; derivated using kriging interpolation function in R; livestock data provided by national agricultural census from 2008

steadily, but after that it remained relatively constant. Subsistence hunting decreased sharply prior to 1995 and was relatively invariable after that (Fig. 2b).

Overlap between Subsistence and Commercial IWU

Classification error differed among IWU (subsistence 0.089, international trade 0.93, and domestic trade 0.203). Overlap accounted for nearly all the classification error in the model, particularly for international trade, for which 88% of the records overlapped with domestic trade (in-bag error 0.88). To a lesser extent (17%), domestic trade also overlapped with subsistence hunting (in-bag error 0.168). In general, the misclassification error rate was low for all IWU categories (<5%, 0.009 for subsistence, 0.05 for international trade, and 0.036 for domestic trade).

The 3 most important variables to classify IWUs were aridity index (GIVI = 243.13), distance to road (183.06), and density of human populations (154.82). Distance to protected area, land uses, and forest cover had similar GIVI values (127.35, 114.90, and 126.21, respectively). Density of livestock had the lowest GIVI value (64.18).

The highest probabilities of subsistence hunting were predicted across a wide area of the country (Fig. 3a). In the south, subsistence hunting covered more continuous areas, including the Amazon forest and nearby table mountains, the Orinoco River delta, and the floodplains

Table 2. Number of animal species and specimens illegally extracted from Venezuela by taxon.

			Extraction rate[a]		*Number of species (number of records)*[b]		
Taxonomic class	*Number of species*	*Number of specimens*	*per specimen*	*in 45 years*	*domestic trade*	*international trade*	*subsistence hunting*
Amphibian	5	233	47	6	3 (3)	4 (10)	2 (2)
Bird	248	777,126	3,134	18,503	149 (773)	139 (1104)	95 (341)
Mammal	93	231,641	2,491	5,515	77 (408)	65 (442)	55 (448)
Reptile	58	7,335,516	126,474	174,655	48 (393	54 (1682)	27 (192)
Total	404	8,344,516		185,434			

[a] *Observed extraction rates calculated as specimens per species and specimens per year for the entire period of study (45 years).*
[b] *Number of species and records of each taxonomic class involved in domestic trade, international trade, and subsistence hunting.*

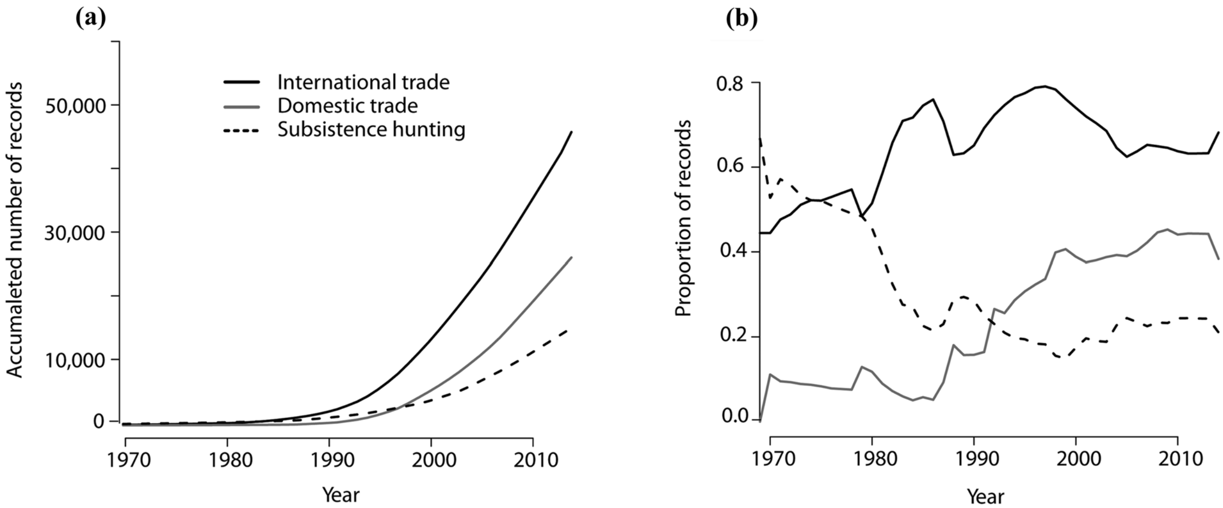

Figure 2. Temporal patterns in records of international trade, domestic trade, and subsistence hunting in Venezuela: (a) accumulated number of records and (b) proportion of type of use reported each year.

north of the Orinoco River. In the west, subsistence hunting had a more fragmented distribution, covering highland areas in the major mountain ranges (the Cordillera de Mérida, the Coastal Cordillera, and the Sierra de Perijá), but subsistence hunting also occurred in lowland areas along the coast. In contrast, domestic trade had a more fragmented distribution: the highest probabilities were predicted in the north, along the coast, and in the lowlands in the center and west (Fig. 3b). Prediction of international trade was more localized and fragmented in the north and somewhat more focused in the west and along the coast (Fig. 3c).

The co-occurrence of subsistence hunting and domestic trade covered a wide area of the country, principally in the central region but throughout the west and Andean region, the central coast, the Orinoco delta, and the south (Fig. 3d). The co-occurrence of domestic and international trade was much more concentrated toward the north, along the coast but also in western inland areas (Fig. 3e). Subsistence hunting and international trade had virtually no co-occurrence (probabilities <0.1; Fig. 3f).

Discussion

Scope and Magnitude of Illegal Wildlife Use

To our knowledge, this is the first study to address the overlap among IWUs from a spatial point of view that generated a tool to evaluate hypotheses about the geographic co-occurrence of commercial and subsistence uses. Ours is also the study to reveal spatial patterns in subsistence and commercial IWU at a country level and thus to allow us quantitative evaluation of the magnitude and overlap of these activities.

Most records were associated with commercial uses, and although enforcement agencies provided a large proportion of them, this should not be taken as an indicator of law-enforcement effectiveness. Particularly in Venezuela, the quality, availability, and completeness of IWU information from governmental agencies is far from satisfactory, mainly because effectiveness of enforcement patrols is low. Poorly trained and motivated staff, insufficient funds and equipment, and lack of coordination among administrative and protection-services agencies

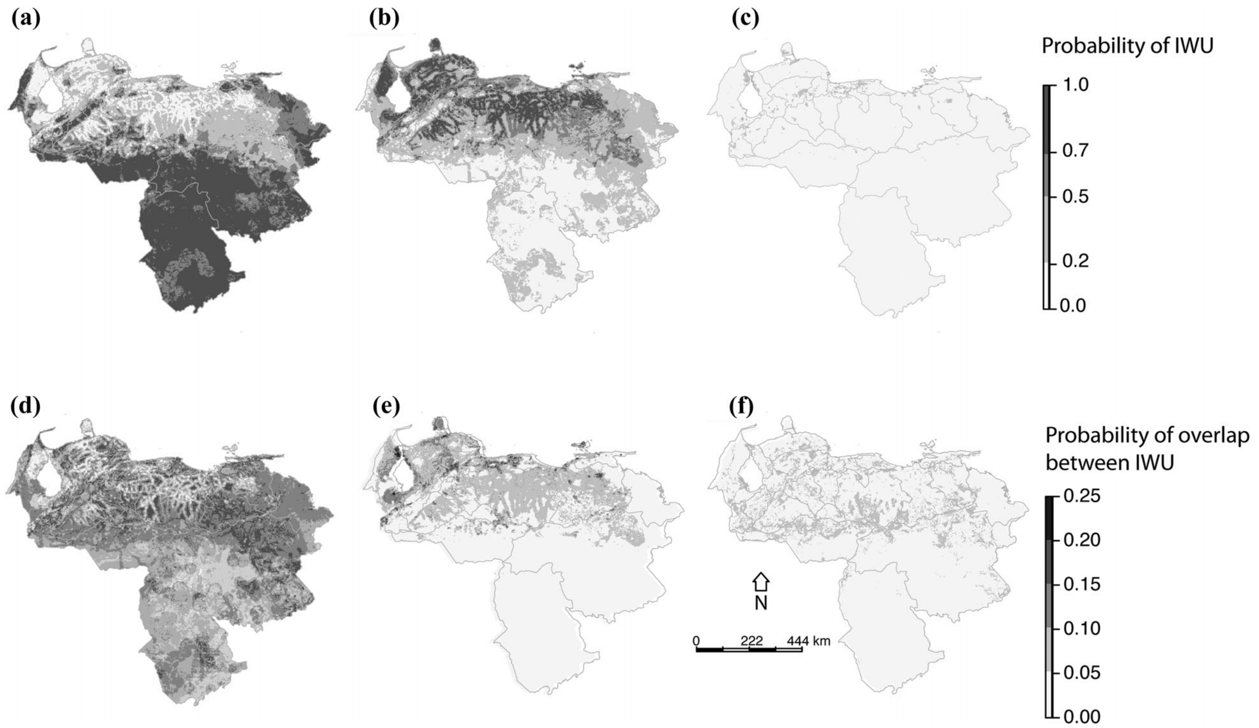

Figure 3. Spatial predictions of illegal wildlife uses (IWU) from the random-forest model: (a) subsistence hunting, (b) domestic trade, and (c) international trade and overlap between (d) subsistence hunting and domestic trade, (e) domestic and international trade, and (f) subsistence hunting and international trade.

(Ojasti 1993) result in a reduced capacity to obtain more realistic, and probably higher, estimates of domestic and international trade. However, that few records were associated with subsistence most likely reflects biased sampling effort. Subsistence records came mostly from anthropological or conservation studies, usually conducted at a local scale and focused on threatened species, so the number of specimens expected is comparatively small. The fact that subsistence hunting is not recognized in the Venezuelan legal framework had a large influence on its detectability, and the scarcity of records says little about the prevalence of trade relative to commercial uses.

Although our estimate of the number of specimens extracted illegally is necessarily an underestimate, it can still serve to point out the importance of a threat that has not been taken sufficiently into account in Venezuela. The observed number of specimens extracted will always be lower than the true total; a standard estimate in criminology is that even the most effective and well-run enforcement programs intercept only 10% of all contraband (Wasser et al. 2007), such that a corrected estimate of the number of specimens affected could be well over 83,000,000 specimens/year. Assuming this detection rate holds in Venezuela is probably overly optimistic. A quantitative assessment of the environmental police in Mexico indicates that the extraction rate for parrots only is 65,000–78,500 parrots/year (Cantú Guzmán et al. 2007). Our estimation of the number of species involved in IWU was more precise given the accumulation of reports over 45 years. The number of species we found that were subjected to IWU was much larger than previous lists (153 species reported by Fergusson [1990]).

Spatial Overlap between Illegal Wildlife Uses

The widespread prevalence of domestic trade suggests that in contrast to international trade, domestic trade does not depend on large markets in cities but rather responds to demand from rural communities. Given how tied international trade appears to be to this domestic trade, the former may be supplied by a network of domestic trade, perhaps using local markets as collection centers, where cross-border dealers acquire goods to transport to neighboring countries (Arroyave Bermudez et al. 2014). The dynamic between domestic and international trade could differ depending on the wildlife in trade and social and economic contexts, for example, from a highly specialized commercial chain, as for *Podocnemis* spp. turtles in Amazon River in Brazil (Pantoja-Lima et al. 2014), to the specialized bird trade in Peru (Daut et al. 2015), to simple and opportunistic trade such as the bushmeat trade in the Abaetetuba open-air market in Brazil (Baía et al. 2010) and the parrot trade in Santa Cruz's markets in Bolivia (Pires & Clarke 2011). Given our broad taxonomic approach, the large extent of spatial dependence in domestic and international trade suggests that both local organizations and sophisticated trader networks may be involved.

In contrast to the large overlap between international and domestic trade, the overlap between subsistence hunting and domestic trade was smaller, yet important. Within the areas of overlap, 2 spatial patterns probably resulted from different anthropic pressures. The first pattern showed a highly aggregated distribution of subsistence hunting and domestic trade in an area where rural and indigenous communities, logging activity (e.g., Imataca forest reserve and Uverito pine plantation), and illegal mining (Ochoa 1997) converge. We suspect the opening up of forest areas in this part of the country by commercial logging and the development of Guri Dam (the country's main hydroelectric) has resulted in an increase in wildlife harvest and trade. There are well-documented examples in other tropical forest of increased depletion of fauna as consequence of commercial logging (Robinson 1999). We do not have direct evidence that this is the case in southern Venezuela, but the scarce evidence suggests that although the annual wildlife harvest by local communities near Imataca is comparatively low (about 12.000 kg/year [Bisbal 1994]), a large percentage of indigenous communities (Pemon, Warao, and Kariña people) consume wildlife and trade wildlife in local economies (Bisbal 1994).

In contrast, the more dispersed pattern of domestic trade in the west and center may reveal a more complex combination of cultural and economic factors, including an increased demand for bushmeat and pets by rural and semirural communities that is being met by a small but widespread network of specialized restaurants and markets (Van Vliet et al. 2014). Although no data exist on how much of the subsistence catch is sold rather than consumed, there are well-documented examples of cultural factors driving the bushmeat market: the sale of threatened marine turtle meat (*Eretmochelys imbricata*, *Geochelone carbonaria*, *G. denticulate, C. mydas*) in rural and urban markets is a longstanding tradition during Lent in Venezuela (Rodríguez 2000). Similarly, the meat of medium and small mammals (e.g., *Tapirus terrestris*, *Tayassu pecari*, *Agouti paca*, and *Dasypus novemcinctus*) is considered particularly flavorful and is sold at urban and rural restaurants across the country at higher prices than domestic meat (Fergusson 1990).

Implications for Conservation

International and national responses to reduce IWU have largely focused on strengthening law enforcement efforts and reducing international consumer demand for illegally sourced wildlife (Gandiwa et al. 2013). However, the overlap between domestic and international we found suggests that much more emphasis should be placed on the role of rural communities to determine the motivations, drivers, dynamics, and responses to IWU (Gray et al. 2015; Roe 2015; Saif et al. 2015).

If IWU has local cultural roots or economic drivers, top-down actions like law enforcement and creation of protected areas alone would be expected to have only modest effects on reducing it (Knapp 2012). Particularly in Venezuela, where 0.06% of gross domestic product is dedicated to environmental conservation and just 350 rangers patrol nearly 150,000 km^2 of protected areas (Rodríguez 2014), it seems unlikely that patrolling can be increased in a way that will result in a meaningful reduction of IWU over an area as large as our model predicts domestic trade to occur. We propose that bottom-up approaches may be more efficient. Actions such as increasing awareness among consumers through education programs (Pellegrini 2001) and community-based natural resource management (Wheeler & Domingo 1997) could more effectively reduce illegal hunting for selected species. Understanding domestic trade may be the key to understanding how IWU works, which underscores the importance of implementing national strategies for monitoring changes in supply and demand over time and space (Challender et al. 2015; Harris et al. 2015; Taylor et al. 2015). Our database presents an opportunity to synthesize current and future data on IWU in Venezuela and other South American countries and to identify information gaps.

Acknowledgments

Funds for this research were provided by the Instituto Venezolano de Investigaciones Científicas. We are grateful to H. Guada, P. Vernet, E. Zent, A. Martínez, A. Fallabrino, D. Giraldon, A.S. Boher, F. Rojas-Suárez, R. Calchi, E. Mujica, A. Cardozo, I. Villasmil, A.C. Molina, P. Ortega, J. Larreal, M.D. Rincón, D. Muller, K. Muller, and T. Barros for providing technical reports, theses, and other grey literature that was not available through online searches. We thank J.R. Ferrer-Paris for helpful discussion on random-forest models and 2 anonymous reviewers for helpful comments on earlier versions of this article.

Supporting Information

A list of published and gray literature included in the database of IWUs (Appendix S1) and a list of species illegally used in Venezuela (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Arroyave Bermudez OY, Romero Goyeneche FJ, Bonilla Gómez A, Hurtado Heredia RG. 2014. Tráfico ilegal de tortugas continentales

(Testudinata) en Colombia: Una aproximación desde el análisis de redes. Acta Biológica Colombiana **19:**381–392.
Asmussen-Soto M. 2010. Estimación del comercio ilegal de fauna silvestre a tres escalas espacio-temporales: Global, regional y nacional. Instituto Venezolano de Investigaciones Científicas. Centro de Estudios Avanzados, Caracas.
Baía JPC, Guimaraes DA, Le Pendu Y. 2010. Non-legalized commerce in game meat in the Brazilian Amazon: a case study. Revista de Biología Tropical **58:**1079–1088.
Bisbal FJ. 1994. Consumo de la fauna silvestre en la zona de Imataca, estado Bolívar, Venezuela. Interciencia **19:**28–33.
Breiman L. 2001. Random forest. Machine Learning **45:**5–32.
Broad S, Mulliken T, Roe D. 2003. The nature and extent of legal and illegal trade in wildlife. Pages 3–22 in Oldfield S, editor. The trade in wildlife: regulation for conservation. Earthscan, London.
Cantú Guzmán JC, Sánchez Saldaña ME, Grosselet M, Silve Gamez J. 2007. The illegal parrot trade in Mexico. A comprehensive assessment. Defenders of Wildlife, Mexico, DF.
Center for International Earth Science Information Network (CIESIN). 2000. Global human population density. Available from http://sedac.ciesin.columbia.edu/data/sets/browse?facets=theme:population (accessed September 2014).
CGIAR Institute. 2010. DIVA-GIS environmental and physic variables. Available from http://www.diva-gis.org/ (accessed October 2014).
Challender DWS, Harrop SR, MacMillan DC. 2015. Understanding markets to conserve trade-threatened species in CITES. Biological Conservation **187:**249–259.
CITES (The Convention on International Trade in Endangered Species of Wild Fauna and Flora). 2009. CITES trade database, UNEP World Conservation Monitoring Centre, Cambridge, UK. Available from http://www.unep-wcmc.org/citestrade/trade.cfm (accessed September 2015).
Congreso de la República de Venezuela. 1970. Ley de protección a la fauna silvestre. Gaceta Oficial Nro 29.289. República de Venezuela, Caracas.
Conteh A, Gavin MC, Solomon J. 2015. Quantifying illegal hunting: a novel application of the quantitative randomised response technique. Biological Conservation **189:**16–23.
Cutler DR, Edwards TC, Beard KH. 2007. Random Forests for classification in ecology. Ecology **88:**2783–2792.
Daut EF, Brightsmith DJ, Mendoza AP, Puhakka L, Peterson MJ. 2015. Illegal domestic bird trade and the role of export quotas in Peru. Journal for Nature Conservation **27:**44–53.
de Merode E, Homewood K, Cowlishaw G. 2004. The value of bushmeat and other wild foods to rural households living in extreme poverty in Democratic Republic of Congo. Biological Conservation **118:**573–581.
Denil M, Trappenberg T. 2010. Overlap versus imbalance. Lecture Notes in Computer Science **6085:**220–231.
DiMiceli C, Carroll ML, Sohlberg RA, Huang C, Hansen, MC. 2011. Annual global automated MODIS vegetation continuous fields (MOD44B) at 250 m spatial resolution for data years beginning day 65, 2000 - 2010, Collection 5 Percent Tree Cover. Available from http://glcf.umd.edu/data/vcf/ (accessed September 2014).
Di Minin E, Laitila J, Montesino-Pouzols F, Leader-Williams N, Slotow R, Goodman PS, Conway AJ, Moilanen A. 2015. Identification of policies for a sustainable legal trade in rhinoceros horn based on population projection and socioeconomic models. Conservation Biology **29:**545–555.
Dongol Y. 2012. A policy gap analysis of Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) implementation in Nepal. Environmental Management DOI **10.100**:62.
Fergusson A. 1990. Aprovechamiento de la fauna silvestre en Venezuela. Cuadernos Lagoven, Caracas.
Franklin J. 2010. Mapping species distributions. Spatial inference and prediction. Cambridge University Press, Cambridge.
Gandiwa E, Heitkonig IMA, Lokhorst AM, Prins HHT, Leeuwis C. 2013. Illegal hunting and law enforcement during a period of economic decline in Zimbabwe: a case study of northern Gonarezhou National Park and adjacent areas. Journal for Nature Conservation **21:**133–142.
Gavin MC, Solomon JN, Blank SG. 2010. Measuring and monitoring illegal use of natural resources. Conservation Biology **24:**89–100.
Golden CD, Wrangham RW, Brashares JS. 2013. Assessing the accuracy of interviewed recall for rare, highly seasonal events: the case of wildlife consumption in Madagascar. Animal Conservation **16:**597–603.
Gray CL, Bozigar M, Bilsborrow RE. 2015. Declining use of wild resources by indigenous peoples of the Ecuadorian Amazon. Biological Conservation **182:**270–277.
Harris JBC, Green JMH, Prawiradilaga DM, Giam X, Giyanto, Hikmatullah GD, Putra CA, Wilcove DS. 2015. Using market data and expert opinion to identify overexploited species in the wild bird trade. Biological Conservation **187:**51–60.
Instituto Nacional de Estadística. 2010. Censo poblacional. Ministerio del Poder Popular de Planificación y Finanzas, Caracas, Venezuela. Available from http://www.ine.gov.ve/ (accessed May 2014).
Kaufmann D, Kraay A, Mastruzzi M. 2011. The worldwide governance indicators: a methodology and analytical issues. Hague Journal on the Rule Law **3:**220–246.
Knapp EJ. 2012. Why poaching pays: a summary of risks and benefits illegal hunters face in Western Serengeti, Tanzania. Tropical Conservation Science **5:**434–445.
Knapp EJ, Rentsch D, Schmitt J, Lewis C, Polasky S. 2010. A tale of three villages: choosing an effective method for assessing poaching levels in western Serengeti, Tanzania. Oryx **44:**178–184.
Lawson K, Vines A. 2014. Global impacts of the illegal wildlife trade. The costs of crime, insecurity and institutional erosion. Chatham House (The Royal Institute of International Affairs), London.
Liaw A, Wiener M. 2002. Classification and regression by randomforest. R News **2:**18–22.
Lindsey PA, et al. 2013. The bushmeat trade in African savannas: Impacts, drivers, and possible solutions. Biological Conservation **160:**80–96.
Machado-Allison, C. 2005. Perfil de la agricultura venezolana. Acta Biológica Venezuelica **25:**7–18.
Maingi JK, Mukeka JM, Kyale DM, Muasya RM. 2012. Spatiotemporal patterns of elephant poaching in south-eastern Kenya. Wildlife Research **39:**234–249.
MFunda I, Røskaft E. 2010. Bushmeat hunting in Serengeti, Tanzania: an important economic activity to local people. International Journal of Biodiversity and Conservation **2:**263–272.
Ministerio del Poder Popular para la Agricultura y Tierras. 2010. Censo agrícola. Available from http://www.mat.gob.ve/CensoAgricola/ (accessed April 2014).
Nasi R, Brown D, Wilkie D, Bennett E, Tutin C, van Tol G, Christophersen T. 2008. Conservation and use of wildlife-based resources: the bushmeat crisis. Technical Series no. 33. Secretariat of the Convention on Biological Diversity, Montreal, and Center for International Forestry Research (CIFOR), Bogor.
Ntiamoa-Baidu Y. 1997. Wildlife and food security in Africa. Food and Agriculture Organization of the United Nations, Rome.
Ochoa J. 1997. Sensibilidades potenciales de una comunidad de mamíferos en un bosque productor de maderas de la Guayana. Interciencia **22:**112–122.
Ojasti J. 1993. Utilización de la fauna silvestre en América Latina. Situación y perspectiva para un manejos sostenible. Guía FAO Conservación 25. Organización de las Naciones Unidas para la Agricultura y la Alimentación, Rome.
Pantoja-Lima J, Aride PHR, De Oliveira AT, Félix-Silva D, Pezzuti JCB, Rebelo GH. 2014. Chain of commercialization of *Podocnemis* spp. turtles (Testudines: Podocnemididae) in the Purus River, Amazon

basin, Brazil: current status and perspectives. Journal of Ethnobiology and Ethnomedicne **10:**2–10.

Pellegrini N. 2001. Educación ambiental en el sistema de parques nacionales de Venezuela. Tópicos en Educación Ambiental **3:** 55–69.

Pires SF, Clarke RV. 2011. Sequential foraging, itinerant fences and parrot poaching in Bolivia. British Journal of Criminology **51:**314–335.

República de Venezuela. 2012. Ley penal del ambiente. Gaceta Oficial Nro 39.913. Caracas.

Robinson JG. 1999. Wildlife harvest in logged tropical forests. Science **284:**595–596.

Rodríguez JP. 2000. Impact of the Venezuelan economic crisis on wild populations of animals and plants. Biological Conservation **96:**151–159.

Rodríguez JP. 2014. Public investment in biodiversity conservation. Interciencia **39:**538-538.

Rodríguez JP, Rojas-Suárez F, Giraldo Herández D. 2010. Libro rojo de los escosistemas terrestres de Venezuela. Provita, Compañía Shell de Venezuela, Lenovo, Caracas.

Roe D. 2015. Conservation, crime and communities: Case studies of efforts to engage local communities in tackling illegal wildlife trade. International Institute for Environment and Development, London.

Saif S, Russell AM, Nodie SI, Inskip C, Lahann P, Barlow A, Barlow CG, Islam A, MacMillan DC. 2015. Local usage of tiger parts and its role in tiger killing in the Bangladesh sundarbans. Human Dimensions of Wildlife **1209:**1–16.

Santos A, Satchabut T, Vigo Trauco G. 2011. Do wildlife trade bans enhance or undermine conservation efforts? Applied Biodiversity Perspective Series **1:**1–15.

SWOT. 2003. The state of the world's sea turtles. Available from http://www.seaturtlestatus.org (accessed February 2014).

Taylor G, et al. 2015. Synthesizing bushmeat research effort in West and Central Africa: A new regional database. Biological Conservation **181:**199–205.

Trabucco A, Zomer R. 2009. Global aridity index (Global-Aridity) and global potential evapo-transpiration (Global-PET). Geospatial Database. Available from http://www.csi.cgiar.org/ (accessed September 2014).

TRAFFIC. 2008. TRAFFIC the wildlife trade monitoring network. Available from http://www.traffic.org/ (accessed February 2014).

Van Vliet N, Quiceno-Mesa MP, Cruz-Antia D, Jonhson L, De Aquino N, Moreno J, Nasi R. 2014. The uncovered volumes of bushmeat commercialized in the Amazonian trifrontier between Colombia, Peru & Brazil. Ethnobiology and Conservation **7:**1–11.

Wasser SK, Mailand C, Booth R, Mutayoba B, Kisamo E, Clark B, Stephens M. 2007. Using DNA to track the origin of the largest ivory seizure since the 1989 trade ban. Proceedings of the National Academy of Sciences of the United States of America **104:**4228–4233.

Wheeler JC, Domingo HR. 1997. Community participation, sustainable use, and vicuña conservation in Peru. Mountain Research and Development **17:**283–287.

Ziegler S, Fa J, Wohlfart C, Streit R, Jacob S, Wegmann M. 2016. Mapping bushmeat hunting pressure in Central Africa. Biotropica **48:**405–412.