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Does hunting or hiking affect wildlife communities in protected areas?

Roland Kays[1,2,3,*], Arielle W. Parsons[1], Megan C. Baker[4], Elizabeth L. Kalies[5], Tavis Forrester[4], Robert Costello[3], Christopher T. Rota[6,7], Joshua J. Millspaugh[6] and William J. McShea[4]

[1]North Carolina Museum of Natural Sciences, 11 West Jones St, Raleigh, NC 27601, USA; [2]Department of Forestry & Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA; [3]Smithsonian's National Museum of Natural History, 10th & Constitution Av NW, Washington, DC 20560, USA; [4]Smithsonian Conservation Biology Institute, 1500 Remount Rd., Front Royal, VA 22630, USA; [5]The Nature Conservancy, Durham, NC 27701, USA; [6]Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, MO 65203, USA; and [7]Division of Forestry and Natural Resources, Wildlife and Fisheries Resources Program, West Virginia University, Morgantown, WV 26506, USA

Summary

1. Managed public wild areas have dual mandates to protect biodiversity and provide recreational opportunities for people. These goals could be at odds if recreation, ranging from hiking to legal hunting, disrupts wildlife enough to alter their space use or community structure.

2. We evaluated the effect of managed hunting and recreation on 12 terrestrial wildlife species by employing a large citizen science camera trapping survey at 1947 sites stratified across different levels of human activities in 32 protected forests in the eastern USA.

3. Habitat covariates, especially the amount of large continuous forest and local housing density, were more important than recreation for affecting the distribution of most species. The four most hunted species (white-tailed deer, raccoons, eastern grey and fox squirrels) were commonly detected throughout the region, but relatively less so at hunted sites. Recreation was most important for affecting the distribution of coyotes, which used hunted areas more compared with unhunted control areas, and did not avoid areas used by hikers.

4. Most species did not avoid human-made trails, and many predators positively selected them. Bears and bobcats were more likely to avoid people in hunted areas than unhunted preserves, suggesting that they perceive the risk of humans differently depending on local hunting regulations. However, this effect was not found for the most heavily hunted species, suggesting that human hunters are not broadly creating 'fear' effects to the wildlife community as would be expected for apex predators.

5. *Synthesis and applications*. Although we found that hiking and managed hunting have measureable effects on the distribution of some species, these were relatively minor in comparison with the importance of habitat covariates associated with land use and habitat fragmentation. These patterns of wildlife distribution suggest that the present practices for regulating recreation in the region are sustainable and in balance with the goal of protecting wildlife populations and may be facilitated by decades of animal habituation to humans. The citizen science monitoring approach we developed could offer a long-term monitoring protocol for protected areas, which would help managers to detect where and when the balance between recreation and wildlife has tipped.

Key-words: camera trap, citizen science, hiking, hunting, mammals, park, protected area, protected forest, recreation, wildlife communities

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[*]Correspondence author. E-mail: Roland.Kays@ncsu.edu

Introduction

Most protected areas have a double mandate to protect natural resources while also allowing recreation (Hammitt, Cole & Monz 2015). This includes nonconsumptive recreation such as hiking, biking and horseback riding, and, in many parts of the world, also consumptive recreation such as managed hunting and trapping. Recreation is important for maintaining public support for protected areas, connecting people with nature (Louv 2005), and is the third largest component of the United States economy, with $646 billion spent annually (Outdoor Industry Association 2012). Recreation could also be a major disturbance to wildlife within protected areas, potentially reducing biodiversity, and thus be counter to natural resource management goals (Hammitt, Cole & Monz 2015).

Unregulated hunting can quickly lead to population declines and extinction (Schipper *et al.* 2008), but the impacts of regulated hunting on wildlife communities are less severe. In North America, restrictions on harvest methods, bag limits and hunting seasons are managed locally with the goal of sustainable harvests (Mahoney & Jackson 2013). Nonetheless, hunting is widespread on the continent with over 13 million participants (Outdoor Foundation 2014), such that human hunters outnumber wolves (*Canis lupus*) and cougars (*Puma concolor*) 165 to 1 (Mech & Peterson 2003; Caso *et al.* 2008). Thus, human hunters could be ecologically acting as predators, having direct (population) and indirect (behavioural) effects on wildlife. Managed hunting has been shown to affect populations of the targeted game species (Behrend *et al.* 1970; Vucetich, Smith & Stahler 2005), but population effects on sympatric species are rarely evaluated. Another unanswered question is the importance of indirect effects of human predators through fear mediated behavioural modifications (Creel & Christianson 2008). Although studies have shown deer change behaviour during short hunting seasons (e.g. Little *et al.* 2015), the longer term behavioural effects of hunting have not been the subject of much study (Cromsigt *et al.* 2013).

Nonconsumptive recreation should have fewer impacts on wildlife in protected areas than hunting or trapping activities, but is still a concern because there are so many more participants (13 million hunters vs. 376 million non-aquatic, nonconsumptive recreationalists in the United States in 2013 (Outdoor Foundation, 2014)). Although some studies have documented the avoidance of hikers by wildlife (Erb, McShea & Guralnick 2012; Hammitt, Cole & Monz 2015), others found prey species attracted to busier trails, presumably using humans as shields against predators (Muhly *et al.* 2011). There are numerous potentially mediating factors, including predator–prey dynamics and habituation to humans, that make it difficult to scale up individual responses to community-wide effects (Tablado & Jenni 2015). One study evaluated the effects of quiet recreation on predators and found an alarming fivefold decline in abundance of four carnivore species in areas that allowed hikers (Reed & Merenlender 2008). The effects of consumptive recreation (hunting and trapping) on wildlife are presumably greater than the quiet non-consumptive recreation studied by Reed & Merenlender (2008), raising the spectre of a potentially large conflict between the preservation and recreation mandates of protected areas. More broad-scale surveys are needed to test the generality of a recreation effects in other regions and species.

We evaluate the relative importance of consumptive and nonconsumptive recreation on the wildlife communities within public forests of eastern North America using camera traps to compare animal use of 1947 sites stratified by their recreation use levels. We surveyed a balanced pairing of public forests with similar habitat but differing in whether they allowed hunting. Within an area, we stratified sites by placing cameras on, near and far from hiking trails. If human hunting activity has strong effects on wildlife communities, we expect to see large differences in their use of paired sites, and if animals avoid humans, we expect them to avoid trails and to be less common in heavily used areas. Most of our data come outside of the main fall hunting season, allowing us to test for the ultimate long-term effects of hunting without the proximate avoidance of active hunters. Finally, we test the hypothesis that there will be an interaction between hunting and hiking leading to animals being more sensitive to all recreating humans in areas where they are hunted.

Materials and methods

SITE SELECTION

We surveyed wildlife at 1947 sites within 32 protected areas across six states (Fig. 1, Table S1 in Supporting Information). We targeted larger protected areas (29 sites were >10 km^2) to ensure that most animals within the area were subjected to the given treatment (hunted or not hunted), and not moving between areas. Most of our sites were selected as 13 pairs having similar habitat and landscapes but differing in whether hunting was allowed or not (Fig. 1). Rock Creek Park conducted their first ever deer cull during our study, but we considered it unhunted because of the restricted hunt area and use of sharpshooters over bait. Two other unhunted areas had no comparable hunted area. All sites were predominantly forested, but varied in elevation (4–1152 m) and in degree of development of the surrounding landscape (0–187 houses km^{-2}).

CITIZEN SCIENCE CAMERA TRAPPING

We recruited and trained 352 volunteer citizen scientists and university students to deploy camera traps within our study areas from 2012 to 2014. Camera surveys were generally run from April to June or August to November, with only 23 camera runs extending into the main deer gun-hunting season in late November. Cameras were deployed in groups of three, with one camera placed on a hiking trail, one 50 m from the trail and one about 200 m from the trail (Fig. 2). Volunteers used Reconyx (RC55, PC800 and PC900)

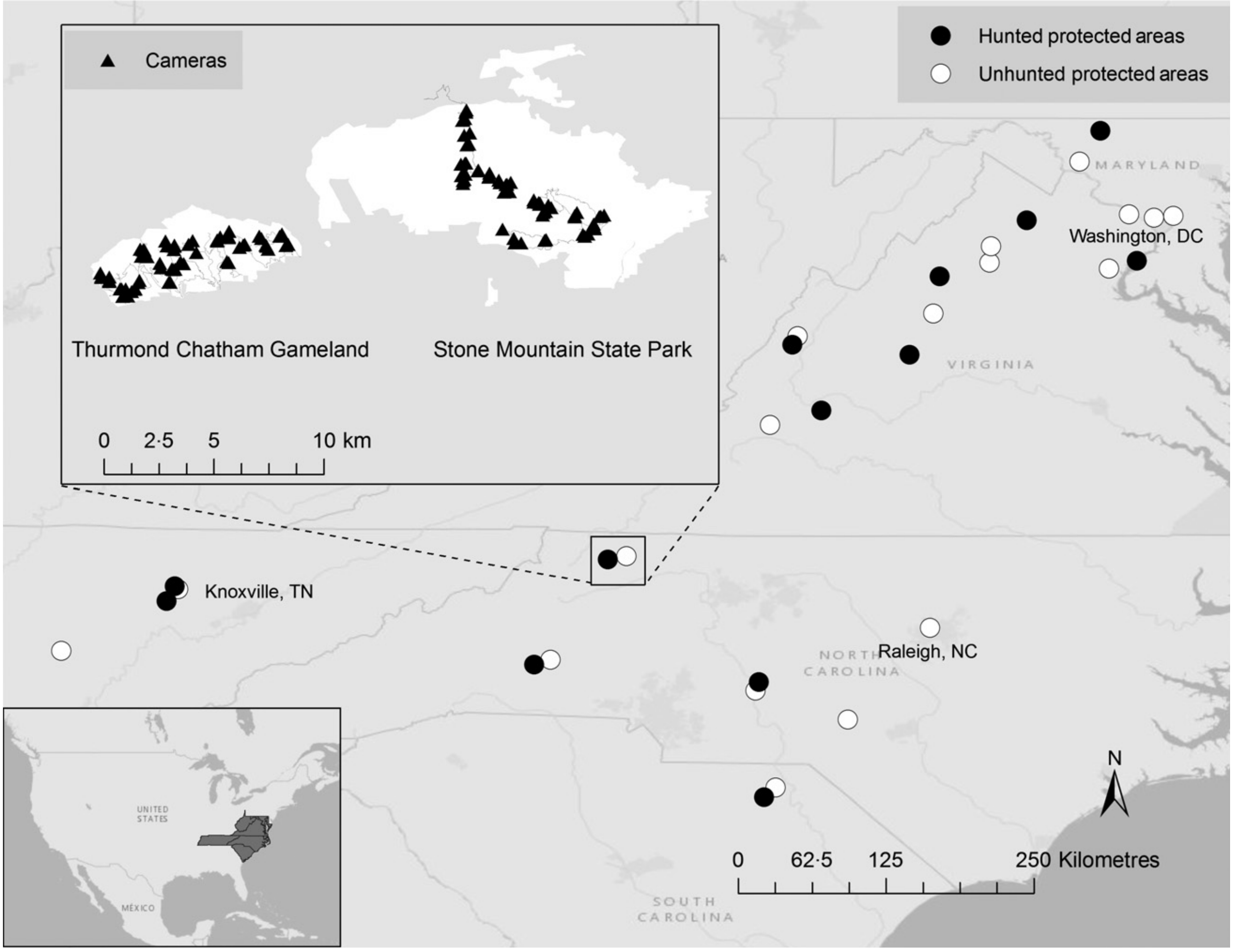

Fig. 1. Map of the 32 protected areas surveyed with inset showing the details of camera trap placements at one pair of sites.

and Bushnell (Trophy Cam HD) camera traps that were equipped with an infrared flash. These cameras all function similarly in having highly sensitive triggers and quick trigger times, allowing them to record animals passing in front of the camera without the addition of bait. Volunteers attached cameras to trees at 40 cm above the ground and returned after 3 weeks to retrieve images and move the cameras. Cameras were set on maximum trigger sensitivity and recorded multiple photographs per trigger, re-triggering immediately if the animal was still in view.

Volunteers used the eMammal software to identify all wildlife species in camera trap images and uploaded pictures to the eMammal Expert Review Tool, where we confirmed or corrected all volunteer species identifications (McShea *et al.* 2016). We grouped consecutive photographs into sequences if they were <60 seconds apart, and used these sequences as independent records for subsequent analysis of detection rate (sequences per day) and occupancy patterns.

COVARIATES

We obtained covariates for each site to test the relative importance of habitat, recreation and land management on wildlife. We also included nuisance covariates in all models to account for variation not directly related to our main hypotheses. We initially considered 46 covariates (Table S1) but reduced those by removing any that were correlated >0·60 and those that performed poorly in univariate exploratory analyses (Table S2). All covariates were mean-centred. The resulting 17 covariates were used in our analyses (Table 1) along with 4 interaction terms.

We used ArcMap (Version 10.1) to obtain habitat covariates for each of our camera sampling points (Table 1). We calculated average housing density in a 5-km radius using the Silvis housing density data set (Hammer *et al.* 2004). We used the Landscape Fragmentation Tool v2.0 (Vogt *et al.* 2007) and the NLCD (Fry *et al.* 2011) to create landcover layers representing the per cent of large core forest and edge habitat in a 5-km radius. We also used the NLCD (Fry *et al.* 2011) to calculate the per cent of agricultural and recently disturbed habitat in a 5-km radius around each camera point. We calculated the distance to the nearest camera site (Nearest_neighbor, NN) to take into account potential spatial autocorrelation effects (Dormann *et al.* 2007). We used the Env-Data tool (Dodge *et al.* 2013) to obtain camera site-level Normalized Difference Vegetation Index (MODIS Land Terra Vegetation Indices 1 km monthly NDVI daily) and average daily camera site-level temperature (ECMWF Interim Full Daily SFC Temperature (2 m above-ground)), precipitation (NCEP NARR Precipitation Rate at Surface) and cloud cover (NCEP-DOE Surface Total Cloud Cover Entire Atmospheric Column).

As a covariate for nonconsumptive recreational use, we used the detection rate for groups of people recorded by our camera traps on trails as a quantitative measure of human use for a protected area. We coded hunting as a categorical yes/no and coded

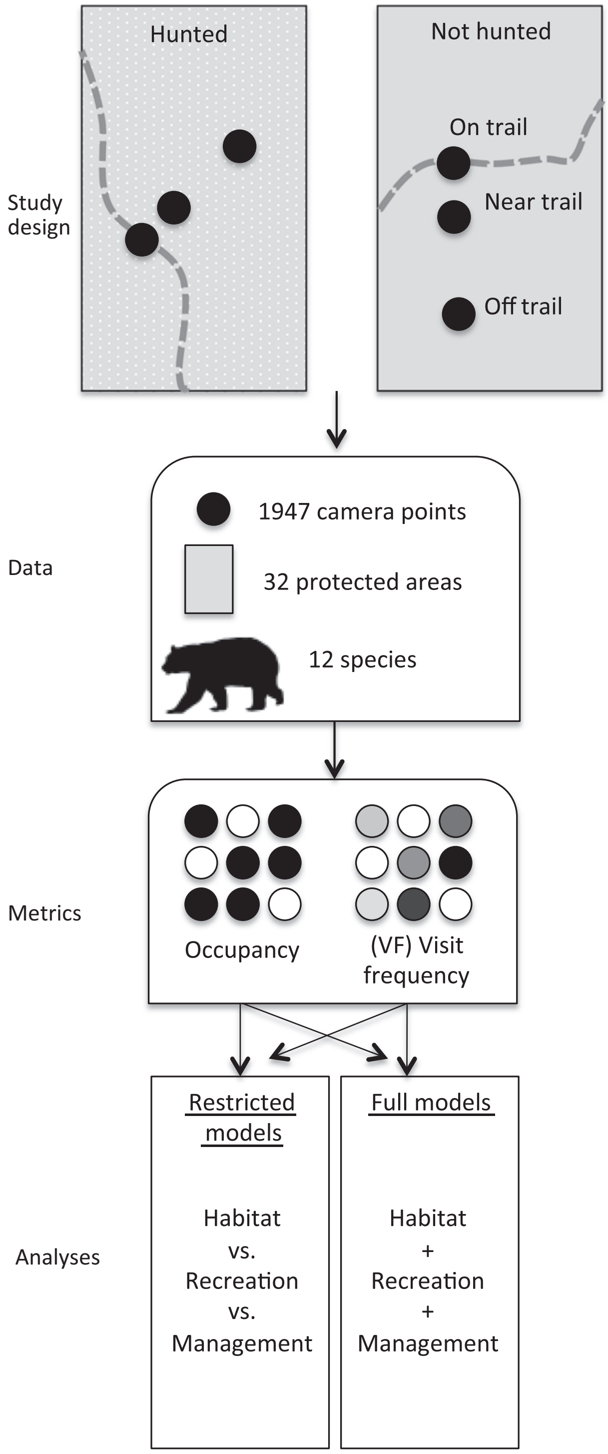

Fig. 2. Schematic of our approach to evaluate the importance of consumptive and nonconsumptive recreation on wildlife in protected areas.

camera distance as a continuous variable describing cameras on (0 m), near (50 m) or far (200 m) from a hiking trail.

To gauge the overall level of hunting for different species in the region, we obtained one year of harvest data from two states (North Carolina Wildlife Resources Commission 2012; Virginia Department of Game and Inland Fisheries 2012). These values were used to rank and understand the overall hunting pressure (high, medium, low) but were not used as covariates in any model.

ANALYTICAL APPROACH

To test hypotheses about the effect of recreation on wildlife, we created models that predict the space use of animals based on data describing the habitat, recreation and management of the protected areas surveyed. As indicators of space use, we analysed two complementary measures from the camera trap data: occupancy and visit frequency (VF) (Fig. 2). Occupancy results describe the probability a site is occupied by a given species and is analysed using a hierarchical model structure that also accounts imperfect detection (MacKenzie *et al.* 2006). VF is simply the detection rate (sequences per day) for a species at a site and is comparable across our sites because we did not use bait, and selected locations in a stratified random design. These measures are complementary in that occupancy describes the geographical spread of a species across the landscape while VF describes the relative degree of use of areas as a reflection of local habitat preference.

For both model types, we evaluated the importance of recreation to the distribution of wildlife by comparing the relative importance of predictor covariates in two ways, using the all-subsets approach. First, we considered the results of restricted models using only covariates from one class of predictor variables (habitat, recreation or management) and compared model performance to test which class of covariates alone was most important. Secondly, we considered combinations of all classes of covariates to create multivariate models that show the combined effects and allowed for interactions (Fig. 2).

OCCUPANCY MODELS

We used the single season occupancy modelling framework of MacKenzie *et al.* (2006) and estimated detection probability (P), defined as the probability of detecting an occurring species at a camera site, and occupancy (ψ), defined as the expected probability that a given camera site is occupied, for each species. We hypothesized that eight covariates could cause heterogeneity in detection probability (hereafter, 'detection covariates'; Table 1). By modelling day and week of sampling, we capture variability in weather and other attributes that are difficult to measure (e.g. changing resource availability), all of which can affect animal behaviour and detectability. We fixed nuisance covariates and tested two detection models, one accounting for people use of a site and one without, coupled with the global occupancy model, to identify the top model of detection per species. We included the nuisance variables LatbyLong and Nearest_neighbor (NN) in all occupancy models, then used the remaining 8 covariates and 4 interactions that we hypothesized could cause heterogeneity in occupancy (hereafter, 'occupancy covariates'), to apply an all-subsets approach using the highest ranked detection model and all combinations of occupancy covariates.

We constructed these models (n = 717 per species) using the RMark package (Laake 2011) and MuMIn package (Bartoń 2014) in R (R Development Core Team 2015). We used quasi-Akaike's Information Criterion (QAIC) for each species due to overdispersion of the global model. For each model, we computed QAIC, difference in QAIC (ΔQAIC) and Akaike weights (wij, weight of covariate i for species j; Burnham & Anderson 2002) and used these values to assess model fit. We ranked relative covariate importance by summing wij, across all models in

Table 1. Covariates used in the visit frequency (VF) and occupancy analyses. Each variable is categorized according to our main hypotheses, including nuisance covariates included to account for variation not directly related to our main hypotheses

Category	Covariate	Description	Type	Model type
Habitat	Ag_5 km	% Agriculture (crop fields) in 5 km neighbourhood[†]	GIS 5 km	Ψ, VF
Habitat	LC_5 km	% Large core (cont. forest frag >5 acre) in 5 km neighbourhood[‡]	GIS 5 km	Ψ, VF
Habitat	Edge_5 km	% Edge (large core) and Perforated (small core) pixels in 5 km neighbourhood[‡]	GIS 5 km	Ψ, VF
Habitat	HDens_5 km	Average Housing Density (houses km^{-2}) in 5 km radius[§]	GIS 5 km	Ψ, VF
Recreation	Cam_distance	Distance camera was placed from a trail (0, 50 or 250 m)	Camera site	Ψ, VF
Recreation	Hunting	Categorical covariate for hunting or no hunting permitted in the park (0,1)	Camera site	Ψ, VF
Recreation	People_site	Total # of people recorded by the camera over the sampling period	Camera site	Ψ, p, VF
Management	Dist_5 km	% Disturbed (burned, logged, grassland conversion) in 5 km neighbourhood[†]	GIS 5 km	Ψ, VF
Nuisance	LatbyLong	Latitude × longitude	Camera site	Ψ, VF
Nuisance	NN	Distance to nearest camera neighbour (m)	Camera site	Ψ, VF
Nuisance	NDVI_site	Moderate Resolution Imaging Spectroradiometer Land Terra Vegetation Indices 1 km monthly NDVI daily; averaged at the site level for the days sampled*	Camera site	p, VF
Nuisance	Cloud	National Center for Environmental Prediction-DOE Surface Total Cloud Cover Entire Atmospheric Column*	Camera site/day	p, VF
Nuisance	Temp	ECMWF Interim Full Daily SFC Temp (2 m above-ground)*	Camera site/day	p, VF
Nuisance	Precip	NCEP NARR Precipitation Rate at Surface*	Camera site/day	p, VF
Nuisance	Week	Week of the year	Camera site/day	p, VF
Nuisance	Year	Year sampled (year 1 or 2)	Camera site	p, VF
Nuisance	Det_dist	Maximum distance at which camera detects animals (m)	Camera site	p, VF

*EnvData (Dodge *et al.* 2013).

[†] GAP landcover data set 2006 (http://gapanalysis.usgs.gov/gaplandcover/).

[‡] Landscape Fragmentation Tool 2006 (http://clear.uconn.edu/%5C/tools/lft/lft2/index.htm).

[§] Hammer *et al.* Landscape and Urban Planning 69 (2004) 183–199 (http://silvis.forest.wisc.edu/old/Library/HousingData.php).

which a given covariate occurred and used cumulative weights to rank relative covariate importance for each species. Larger values of wij are indicative of greater importance for covariate i relative to other covariates in the model (Burnham & Anderson 2002). We considered $wij \geq 0{\cdot}50$ indicative of a strong occupancy response to the covariate and $wij < 0{\cdot}50$ a weak response. We also calculated model-averaged parameter ($\tilde{\tilde{\beta}}_j$) estimates and unconditional standard errors (SE) for each covariate across models with ΔQAIC <4 to assess the direction of response by each species. For each species, we estimated ψ using the top ranked model.

VISIT FREQUENCY MODELS

We assumed the number of detections of each species obtained at camera trap site *i* was a Poisson random variable:

$$y_i \sim \mathrm{Poisson}(\lambda_i) \qquad \text{eqn 1}$$

We modelled the expected number of photographs at site *i* as a loglinear model:

$$\log(\lambda_i) = x_i\boldsymbol{\beta} + \mathrm{offset}_i + \varepsilon_i,$$

where $\mathbf{x}_i$ is a vector of covariates and $\boldsymbol{\beta}$ is a conformable vector of slope parameters; the offset term is equal to the log of the number of days camera trap *i* operated; and $\varepsilon \sim \text{iid } N(0, \sigma^2)$ and is meant to capture additional variation in the number of detections of each species. We assumed independent normal prior distributions for the slope parameters ($\boldsymbol{\beta} \sim$ multivariate normal $(0, 10\mathbf{I})$, and we assumed a uniform prior distribution for the random error standard deviation parameter ($\sigma \sim$ Uniform (0, 10)).

We assessed model fit with posterior predictive checks (PPC) (Kéry & Schaub, 2012, Gelman *et al.*, 2014). Briefly, we calculated the sum of squared Pearson residuals from observed data ($T(y)$) and from data simulated assuming model (1) was the data-generating model ($T(y_{\mathrm{sim}})$). We calculated a Bayesian *P*-value as $p\mathrm{B} = \Pr(T(y_{sim}) > T(y))$ from posterior simulations and assumed adequate fit if $0{\cdot}1 < p\mathrm{B} < 0{\cdot}9$.

We ran a set of 5 visit frequency (VF) models for each species (Table S8). We fit VF models in OpenBUGS v3.2.3 (Lunn *et al.*, 2000) via R2OpenBUGS v3.2 (Sturtz, Ligges & Gelman, 2005) in R v3.1.0 (R Core Team, 2015). We based inference on posterior samples generated from three markov chains. We used trace plots to determine an adequate burn-in phase. After discarding burn-in samples, we saved every 10th sample and ran simulations until all chains adequately converged ($\hat{R} \leq 1{\cdot}1$ (Gelman *et al.*, 2014, p. 287)).

Results

CAMERA SURVEY DATA

Over 42 872 camera nights, we obtained 30 975 detections of people and 53 372 detections of wildlife. There were 12 species with at least 200 detections, which we considered the minimum necessary to ensure model convergence: eastern chipmunk (*Tamias striatus*, hereafter 'chipmunk'), coyote (*Canis latrans*), American black bear (*Ursus americanus*, hereafter 'bear'), bobcat (*Lynx rufus*), gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*), white-tailed deer (*Odocoileus virginianus*, hereafter 'deer'), wild turkey (*Meleagris gallopavo*, hereafter 'turkey'), northern raccoon (*Procyon lotor*, hereafter 'raccoon'), eastern gray squirrel (*Sciurus carolinensis*, hereafter 'gray squirrel'), eastern fox squirrel (*Sciurus niger*, hereafter 'fox squirrel') and Virginia opossum (*Didelphis virginiana*, hereafter 'opossum').

HARVEST DATA

State harvest records for the region show high (>100 000 killed year^{-1}) hunting levels for deer and gray squirrels, medium intensity (10 000–100 000) harvest of raccoon, fox squirrel, coyote and turkey, and a low (<10 000) harvest of foxes, bobcat and bear (Fig. S1). Opossums can be harvested in both states but no records are kept, and hunting pressure is presumed to be low. Chipmunks are not game species in the region and can only be legally taken through special nuisance permits.

RESTRICTED MODEL RESULTS

The restricted model sets present the results of using variables from one class of covariates for both occupancy and VF and showed that habitat alone explained the distribution of most species better than recreation or management alone (Table 2).

The top occupancy models for most species (bear, bobcat, chipmunk, coyote, fox squirrel, gray fox, opossum, red fox, Turkey) performed well as they ranked higher than the associated null models (which had ΔQAIC values ranging from 11 to 202). Occupancy models did not perform as well (ΔQAIC < 3 compared with null model) for the three more ubiquitous species (gray squirrel, deer and raccoon) because there was little variation to be explained (i.e. the species occupied most sites).

Our models of VF showed strong relationships and good fit ($0{\cdot}1 < p\mathrm{B} < 0{\cdot}9$) for all species, most of which had had strong habitat associations. Coyotes, deer and fox squirrel had recreation as the top VF model, while the null model, including only nuisance variables, was best for gray fox and chipmunk.

FULL MODEL RESULTS

The full multivariate occupancy (Table 3, Tables S3–S6) and VF (Table 4, Tables S7–S11) models for most species included habitat and recreation covariates, showing that both types of variables have some effects on animal distribution. Hunting had a negative effect for the four most hunted species (deer, raccoon, gray and fox squirrels) but a positive effect for coyotes and turkeys. Hiking trails were not a significant factor for most species, but were positively associated with coyote and bobcat VF.

The most important habitat factors across the animal community were an interaction effect between housing density and large core forests, which was detected with both modelling approaches (Tables 3–4). In all cases, this interaction was due to a change in the relationship at higher housing density where there were no large core forests, and some more sensitive species were absent. A number of species moderately well adapted to humans (deer, raccoons, fox squirrels and opossums) were negatively associated with large core forests, positively associated with low-density housing and negatively associated with high-density housing (Table 5). Red foxes were the most specialized urban species in our study, with positive associations towards houses at both scales, and an avoidance of large natural areas. Bobcats were the most specialized wilderness species in our study, with a positive association with large core forests and a negative association with houses. Similar relationships were seen in the occupancy results, except that deer and red fox were positively associated with high housing density, turkeys were positively associated with large core forests, and fox squirrels were

Table 2. Results from restricted model sets predicting the occupancy and visit frequency of sites within protected areas by twelve wildlife species. These models use only covariates related to habitat, recreation or management of the area. Values reported here are the differences in QAIC (occupancy models) or DIC (visit frequency models) scores compared with the top restricted model; thus, zero represents the best restricted model and those that performed worse have higher values. Covariates used in each model set are described in Table 1

	Gray squirrel	Deer	Raccoon	Fox squirrel	Coyote	Turkey	Gray fox	Red fox	Bobcat	Bear	Opossum	Chipmunk
Occupancy models												
Habitat	0	0	0	0	14	2	0	0	0	0	0	0
Recreation	4	2	3	111	0	0	9	37	84	92	11	35
Management	5	2	4	44	17	10	15	56	94	35	10	35
Null	3	0	3	203	17	36	81	116	135	133	12	60
Visit frequency models												
Habitat	0	23	0	32	93	0	29	0	0	0	0	10
Recreation	93	0	62	0	0	26	52	107	74	9	176	3
Management	24	20	7	33	31	30	35	95	156	36	84	13
Null	28	25	54	22	168	24	0	72	51	117	47	0

Table 3. Full multivariate occupancy model results for 12 species summarized to show which environmental covariates had significant positive (+) or negative (–) relationships with the model-averaged coefficients. Significant interaction terms are indicated with a (*); see the text and graphs for a discussion of the direction of their effects. Cell shading separates the predictor covariates into habitat (top), recreation (mid) and land management categories (bottom)

	Gray squirrel	Deer	Raccoon	Fox squirrel	Coyote	Turkey	Gray fox	Red fox	Bobcat	Bear	Opossum	Chip.
HDens_5km										–		
Ag_5km				+				–	+	+	+	+
LC_5km												
Edge_5km	–			+							–	
LC_5km X HDens_5km		*	*	*	*	*		*	*		*	
Trail	+				+							
Hunting				–	+	+						
People_site			–									
HuntingXPeople_site								*	*	*		
TrailXPeople_site						*			*			*
Managed Habitat (Dist_5km)				–			+	–	–	–	+	

Table 4. Full multivariate visit frequency model results for 12 species summarized to show which environmental covariates had significant positive (+) or negative (–) relationships in the model average coefficients. Significant interaction terms are indicated with a (*); see the text and graphs for a discussion of the direction of their effects. Cell shading separates the predictor covariates into habitat (top), recreation (mid) and management categories (bottom)

	Gray squirrel	Deer	Raccoon	Fox squirrel	Coyote	Turkey	Gray fox	Red fox	Bobcat	Bear	Opossum	Chip.
HDens_5km										–		
Ag_5km	+	–		+				–	+	+	+	+
LC_5km										+		+
Edge_5km	+			+		–			+		–	+
LC_5km X HDens_5km	*	*	*	*		*		*	*		*	
Trail					+				+			
Hunting	–	–	–	–	+	+	+					
People_site												
HuntingXPeople_site								*	*	*		
TrailXPeople_site	*											
Managed Habitat (Dist_5km)	–			–			+		–	–	+	

Table 5. Significant positive (+) or negative (–) relationships between wildlife, housing density and large core forests from visit frequency models accounting for an interaction between the two covariates. Similar results were found in occupancy models (Table S11)

	Low regional housing density		High regional housing density
	Housing density	Large core forests	Housing density
Deer	+	–	–
Bear	–	+	–
Fox squirrel	+	–	–
Opossum	+	–	–
Red fox	+	–	+
Bobcat	–	+	+
Gray squirrel	+	+	+
Turkey	+	–	–

significantly associated with houses and negatively associated with large core forests (Table S11).

For three carnivores, we also found an interaction between the species response to people on trails and the hunting status of a site (Fig. 3, Tables 3–4). Red foxes had higher occupancy and VF at sites with high use by people, and this relationship was stronger in hunted areas. Bear and bobcat both avoided trails more strongly at hunted sites; these sites had substantial difference in the rate that people used the trails, which we suspect may have contributed to the significance of this interaction term. Four species also showed statistical interactions between trails and people, reflecting different slopes in their response to the drastically different detection rates of people on and off trails. Turkeys, chipmunks and bobcats had lower occupancy rates at heavily hiked trails (Table 3), while gray squirrels had higher visit frequency on trails heavily used by people (Table 4).

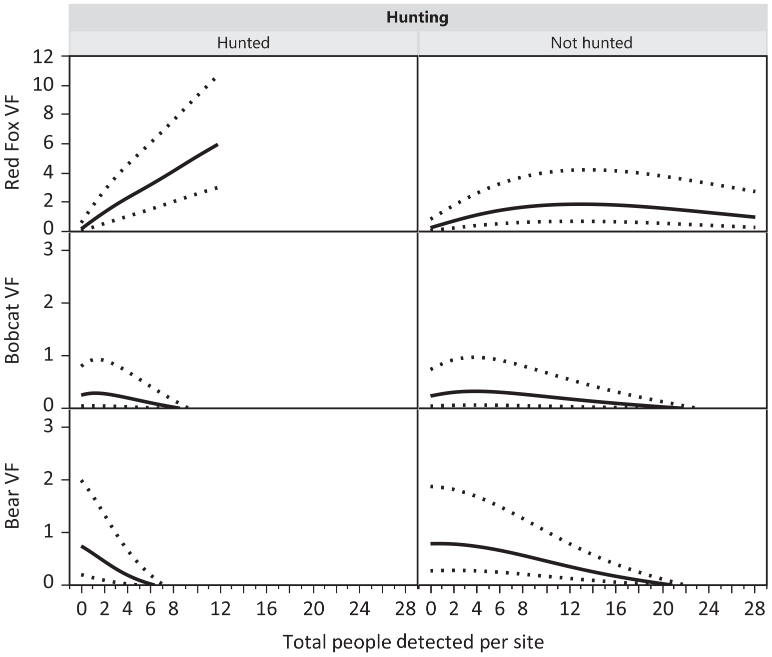

Fig. 3. Visit frequency (VF) model results showed that three species of wildlife responded to the human use of trails differently in hunted and unhunted areas. Red fox increased their use of trails with high human traffic (groups of people detected during 3-week survey) in all sites, but this was stronger in hunted areas. Bobcats and bears both had a stronger avoidance of people in hunted areas. Dotted lines are 95% credible intervals for VF models.

The results of our full occupancy and VF models were generally similar. Of 50 significant variable associations, only one had opposite predictions from the different modelling approaches, edge habitat for gray squirrel. Across all species our occupancy models detected seven significant relationships not present in the VF models, the VF approach produced 11 significant relationships not found in the occupancy models, and the two approaches have similar significant predictions for 29 covariates.

Discussion

Although other studies have found isolated negative impacts of recreation on animal behaviour (Hammitt, Cole & Monz 2015), there have been few studies on community-wide impacts (Reed & Merenlender 2008), and none that integrated the evaluation of both consumptive and nonconsumptive recreation. Our broad-scale survey, in collaboration with citizen scientists, shows that the impact of recreational use on wildlife communities in public areas is relatively minor. For most species, habitat factors were more important than recreation in models predicting their distribution and habitat preferences. Comparing types of recreation, hunting appeared to have more influence than hiking on wildlife species, as hunted sites were correlated with a decrease in activity of the four most hunted species, while fewer species avoided hiking trails. Nonetheless, these hunted species remain common throughout the region. Although we did not consider finer points of population vital rates, animal stress or changes to species interactions, our broad comparisons of animal distribution suggest that recreational use of our public areas, as presently managed in the region, is not having a widespread harmful effect on wildlife communities.

HABITAT ASSOCIATIONS

Our modelling results support previous work of species sensitivity to habitat type and development (Lesmeister *et al.* 2015). Across species, the most important habitat features were large unfragmented forests and the housing density surrounding the protected area. Bears and bobcats were primarily associated with the more wild areas with few houses and large unfragmented forests. Contrasting this, most other wildlife species (deer, raccoon, fox squirrel, gray squirrel, opossum, red fox) had higher occupancy and a preference for using protected areas within more fragmented habitat and surrounded by moderate densities of houses. The amount of agriculture surrounding protected areas was positively associated with a number of wildlife species, while heavily managed lands more often had a negative association for forest species.

HUNTING EFFECTS

Results from our restricted model sets and variable weights suggest that, across this animal community, hunting is secondary in importance to habitat covariates in determining animal occupancy and habitat use. However, there was some important effects as the four most heavily harvested species in our study (gray squirrel, deer, raccoon and fox squirrel) had negative relationships between hunting and their visit frequency, although this was not a predictor of their occupancy (except fox squirrel). None of these widespread species are of conservation concern; indeed, deer overabundance is more likely to cause damage to vegetation communities, or cause conflict with people (McShea 2012). Many protected areas encourage hunting with the goal of reducing the impact of deer on natural resources of the public area or the surrounding landscape, and our results suggest this is occurring. However, the effect was variable across the region, and of moderate biological significance, with an average increase of 3·1 deer (SE = 2·3) detected per 3 week deployment and no reduction in their occupancy.

The species showing the strongest relationships with recreation covariates for both occupancy and VF was the coyote. Surprisingly, these were positive associations, with more coyote activity in hunted areas and a preference for using hiking trails. Some coyotes are harvested for fur, but the primary motivation by most coyotes hunters is to reduce the local coyote population (Stevens, More & Glass 1994). Coyote removal experiments suggest this strategy is not effective, probably because it disrupts their social system, which encourages dispersing animals to settle in the area (Kilgo *et al.* 2014). Although we did not estimate coyote density, our higher values for coyote occupancy and VF in hunted areas support this hypothesis and suggest that managers seeking fewer coyotes in an area should encourage stable packs which, in turn, might discourage dispersing animals from settling in an area (Maletzke *et al.* 2014).

IMPACTS OF RECREATIONAL TRAIL USE

Our comparison of animal activity on, near and far from trails did not find strong or consistent avoidance of hiking trails by most wildlife. Indeed, most predatory species were actually detected most often on trails, although at night, when few human are using trails. This trail preference of predators has been noted for numerous tropical species (Harmsen *et al.* 2010; Kays *et al.* 2010). Although they did not avoid trails per se, four species (raccoon, bear, turkey and bobcat) avoided the most heavily used trails while (red foxes and gray squirrels) actually had higher VF at busy trails, perhaps using humans as shields against predators (Muhly *et al.* 2011). A previous study of wildlife in the same region found similar results for black bears and red foxes (Erb, McShea & Guralnick 2012). However, even our most heavily used trails (>100 groups of people day^{-1}) were used by wildlife including deer (11/15 sites), coyotes (8/15), gray squirrels (7/15) and red fox (5/15).

Our lack of a consistent strong relationship between trail use and wildlife communities is counter to the startling decrease in abundance of four predator species in recreational areas in California found by Reed & Merenlender (2008). While all of our sites had some public recreation, their study contrasted public recreation sites with private land where recreation was forbidden, which could explain the difference in our results. Additionally, the eastern forests we surveyed are denser than the oak woodland habitat of the California study, which might offer animals more cover and seclusion from hikers. Finally, there could be differences in level that wildlife has habituated to people across the country.

INTERACTIONS BETWEEN HUNTING AND HIKING

Although a variety of studies have shown behavioural responses of wildlife to hikers (Hammitt, Cole & Monz 2015) and hunters (e.g. Little *et al.* 2015), none have considered both at once, and none have evaluated the implications of these responses on the community composition and habitat preference outside of the hunting season. The absence of strong spatial avoidance of recreationalists suggests that many species are habituated to humans in protected areas, even where hunted. This habituation was also shown by a recent analysis of animal behaviour from the same camera trap data set we analysed here, which showed decreased vigilance for deer in areas with high levels of recreation (S.G. Schuttler, A.W. Parsons, T. Forrester, M.C. Baker, W.J. McShea, R. Costello & R. Kays, personal communication).

We predicted that if hunters maintain a landscape of fear for wildlife towards people (*sensu* Laundre, Hernandez & Ripple 2010), habituation of wildlife to people would be greater in unhunted areas. We found some support for this in our two most wilderness-dependent species, bobcats and bears, which had a moderately sharper avoidance of people in hunted areas. The slight nature of this relationship, and its absence in other more heavily harvested species, suggests that human hunters are not having a strong indirect effect on most prey behaviours as would be expected from native apex predators, probably because of the limited hunting season (Cromsigt *et al.* 2013).

OCCUPANCY AND VISIT FREQUENCY

To evaluate the effect of recreation on wildlife, we used two separate metrics of space use derived from the same camera trap data set: occupancy and visit frequency (VF). While occupancy modelling is well-established (MacKenzie *et al.* 2006), using VF (i.e. the raw detection rate) is more controversial (Jennelle, Runge & MacKenzie 2002). However, there are two factors that differ between our approach and some previous efforts. First, we used a consistent field methodology, with no bait, in a stratified random design to avoid many of the potential biases discussed by Sollmann *et al.* (2013). Secondly, we interpret the VF metric not as a measure of abundance, but as an indication of local habitat preference that offers a simple measure of relative habitat use. This innovative approach uses these two metrics as complementary measures of animal distribution (occupancy) and habitat preference (VF).

Our models using the same sets of covariates to predict occupancy and VF gave similar results for most species. However, the VF models performed better (vs. null model) for the most ubiquitous species, which had very high occupancy rates at all study sites and therefore less variation in the presence/absence context of occupancy modelling. Disparities between the two modelling approaches may in part reflect a reduced sensitivity of the occupancy approach caused by the reduction of a continuous variable used in VF (detection rate) into a categorical variable (occupied or not), or the hierarchical nature of occupancy, which helps account for imperfect detection. Additionally, environmental factors could have different influences on occupancy vs. local habitat preferences. Regardless, both approaches were consistent in showing that recreation had relatively minor effect on the distribution and habitat preferences for most wildlife species. We recommend this complementary analytical approach for quantifying the relative importance of environmental factors affecting wildlife species that cannot be identified to the individual for use with capture–recapture density estimators.

MANAGEMENT IMPLICATIONS

The impact of recreation on wildlife in protected areas is an important question that relates not only to management of protected areas, but also to how modern society connects to nature through recreation. Given the huge economic contributions of the outdoor industry ($646 billion annually, Outdoor Industry Association 2012), this issue also has significant economic implications. Our large-scale study, enabled by citizen science surveys, is broadly relevant because the 32 protected areas we included had a wide variety of management practices and degree of use by humans. These areas are typical for the country in either permitting seasonal hunting or not, and in allowing trail-based recreation by hikers, bicyclists and/or horseback riders. We found human trails were not widely avoided by most species of wildlife, suggesting that the relatively sparse recreation trail networks typical of this region are not having negative effects on the broader wildlife community. Our results show the managed wildlife harvest of some protected areas can marginally reduce the activity levels (VF) of the most hunted species (deer, raccoons and gray squirrels), but do not affect their occupancy levels, and have little impact on the distribution of most other wildlife species. Hunting is often encouraged by managers to reduce the negative ecological impacts of deer populations; our results suggest the present level of harvest in most areas is resulting in variable but significant impacts on local deer habitat preferences (VF) but not on their occupancy. Furthermore, our results showing an increase in coyote activity in hunted areas suggest that direct persecution aimed to reduce their populations may have the reverse effect, possibly due to more immigrants filling the territories vacated by hunted animals (Kilgo *et al*. 2014).

We acknowledge that recreation could still be affecting more subtle aspects of the wildlife populations, such vital rates or animal stress; however, we suggest that if these resulted in important population level differences in distribution or abundance, we would have detected them with our analyses. Additionally, we think the citizen science monitoring approach we developed could offer a sustainable long-term monitoring protocol for protected areas, which would help them detect where and when the balance between recreation and wildlife has tipped.

Our results suggest that present levels of managed wildlife harvest and nonconsumptive recreation in the region are sustainable, without significant negative impacts to the distribution patterns of the broader wildlife community. Connecting the public with their natural resources through encouraging its recreational use is not contradictory, within the bounds of existing regulations. This finding offers hope for maintaining wildlife diversity in the United States and for the future of wildlife in any part of the world where animal harvest is managed and people look to protected areas as a place they can escape to enjoy nature without harming it in the process.

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Data accessibility

All camera trap data used in this study are available through eMammal.org and the Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.gv1dq (Kays *et al*. 2016).

References

Bartoń, K. (2014) *MuMIn: Multi-Model Inference, version 1.10.0*. https://cran.r-project.org/web/packages/MuMIn/index.html.

Behrend, D.F., Mattfeld, G.F., Tierson, W.C. & Wiley, J.E. III (1970) Deer density control for comprehensive forest management. *Journal of Forestry*, **68**, 695–700.

Burnham, K.P. & Anderson, R.D. (2002) *Model Selection and Multi-Model Inference*. Springer, New York.

Caso, A., Lopez-Gonzalez, C., Payan, E., Eizirik, E., de Oliveira, T., Leite-Pitman, R., Kelly, M., Valderrama, C. & Lucherini, M. (2008) *Puma Concolor*. *The IUCN Red List of Threatened Species*, Version 20.

Creel, S. & Christianson, D. (2008) Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, **23**, 194–201.

Cromsigt, J.P.G.M., Kuijper, D.P.J., Adam, M., Beschta, R.L., Churski, M., Eycott, A. *et al*. (2013) Hunting for fear: innovating management of human-wildlife conflicts. *Journal of Applied Ecology*, **50**, 544–549.

Dodge, S., Bohrer, G., Weinzierl, R., Davidson, S.C., Kays, R., Douglas, D. *et al*. (2013) The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. *Movement Ecology*, **1**, 1–14.

Dormann, C.F., McPherson, J.M., Araujo, M.B., Bivand, R., Bolliger, J., Carl, G. *et al*. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, **30**, 609–628.

Erb, P.L., McShea, W.J. & Guralnick, R.P. (2012) Anthropogenic influences on macro-level mammal occupancy in the Appalachian trail corridor. *PLoS One*, **7**, e42574.

Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., Barnes, C., Herold, N. & Wickham, J. (2011) Completion of the 2006 National Land Cover Database for the Conterminous United States. *Photogrammetric Engineering and Remote Sensing*, **77**, 858–864.

Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A. & Rubin, D.B. (2014) *Bayesian Data Analysis*, 3rd edn. CRC Press.

Hammer, R.B., Stewart, S.I., Winkler, R., Radeloff, V.C. & Voss., P.R. (2004) Characterizing spatial and temporal residential density patterns across the U.S. Midwest, 1940–1990. *Landscape and Urban Planning*, **69**, 183–199.

Hammitt, W.E., Cole, D.N. & Monz, C.A. (2015) *Wildland Recreation: Ecology and Management*. John Wiley & Sons, Oxford, UK.

Harmsen, B.J., Foster, R.J., Silver, S., Ostro, L. & Doncaster, C.P. (2010) Differential use of trails by forest mammals and the implications for camera-trap studies: a case study from Belize. *Biotroica*, **42**, 126–133.

Jennelle, C.S., Runge, M.C. & MacKenzie, D.I. (2002) The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. *Animal Conservation*, **5**, 119–120.

Kays, R., Tilak, S., Kranstauber, B., Jansen, P.A., Carbone, C., Rowcliffe, M., Fountain, T., Eggert, J. & He, Z. (2010) Monitoring wild animal communities with arrays of motion sensitive camera traps. *International Journal of Research and Reviews in Wireless Sensor Networks*, **1**, 19–29.

Kays, R., Parsons, A.W., Baker, M.C., Kalies, E.L., Forrester, T., Costello, R., Rota, C.T., Millspaugh, J.J. & McShea, W.J. (2016) Data from: Does hunting or hiking affect wildlife communities in protected areas? *Dryad Digital Repository*, http://dx.doi.org/10.5061/dryad.gv1dq.

Kery, M. & Schaub, M. (2012) *Bayesian Population Analysis using WinBUGS: A Hierarchical Perspective*. Academic Press, Waltham, MA, USA.

Kilgo, J.C., Vukovich, M., Scott Ray, H., Shaw, C.E. & Ruth, C. (2014) Coyote removal, understory cover, and survival of white-tailed deer neonates. *The Journal of Wildlife Management*, **78**, 1261–1271.

Laake, J. (2011) *RMark: R Code for MARK Analysis, version 2.0.7*. https://cran.r-project.org/web/packages/RMark/index.html.

Laundre, J.W., Hernandez, L. & Ripple, W.J. (2010) The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal*, **3**, 1–7.

Lesmeister, D.B., Nielsen, C.K., Schauber, E.M. & Hellgren, E.C. (2015) Spatial and temporal structure of a mesocarnivore guild in midwestern north America. *Wildlife Monographs*, **191**, 1–61.

Little, A.R., Demarais, S., Gee, K.L., Webb, S.L., Riffell, S.K., Gaskamp, J.A. & Belant, J.L. (2015) Does human predation risk affect harvest susceptibility of white-tailed deer during hunting season? *Wildlife Society Bulletin*, **38**, 797–805.

Louv, R. (2005) *Last Child in the Woods, Saving Our Children from Nature-Deficit Disorder*. Algonquin Books of Chapel Hill, NC, USA.

Lunn, D.J., Thomas, A., Best, N. & Spiegelhalter, D. (2000) WinBUGS – a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing*, **10**, 325–337.

MacKenzie, D., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L. & Hines, J.E. (2006) *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Academic Press, New York, USA.

Mahoney, S.P. & Jackson, J.J. (2013) Enshrining hunting as a foundation for conservation – The North American Model. *International Journal of Environmental Studies*, **70**, 448–459.

Maletzke, B.T., Wielgus, R., Koehler, G.M., Swanson, M., Cooley, H. & Alldredge, J.R. (2014) Effects of hunting on cougar spatial organization. *Ecology and Evolution*, **4**, 2178–2185.

McShea, W.J. (2012) Ecology and management of white-tailed deer in a changing world. *Annals of the New York Academy of Sciences*, **1249**, 45–56.

McShea, W.J., Forrester, T., Costello, R., He, Z. & Kays, R. (2016) Volunteer-run cameras as distributed sensors for macrosystem mammal research. *Landscape Ecology*, **31**, 55–66.

Mech, L.D. & Peterson, R.O. (2003) Wolf-prey relations. *Wolves: Behavior, Ecology, and Conservation* (eds L.D. Mech & L. Boitani), pp. 131–160. University of Chicago Press, Chicago, Illinois.

Muhly, T.B., Semeniuk, C., Massolo, A., Hickman, L. & Musiani, M. (2011) Human activity helps prey win the predator-prey space race. *PLoS One*, **6**, e17050.

North Carolina Wildlife Resources Commission (2012) 2011-12 Harvest Survey of North Carolina Hunters.

Outdoor Foundation (2014) *Outdoor Participant Report*.

Outdoor Industry Association (2012) *The Outdoor Recreation Economy*.

Reed, S.E. & Merenlender, A.M. (2008) Quiet, nonconsumptive recreation reduces protected area effectiveness. *Conservation Letters*, **1**, 146–154.

R Development Core Team. (2015) *R: A Language and Environment for Statistical Computing, version 3.1.2*. R Foundation for Statistical Computing, Vienna, Austria.

Schipper, J, Chanson, J.S., Chiozza, F, Cox, N.A., Hoffmann, M, Katariya, V. (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science (New York, N.Y.)*, **322**, 225–230.

Sollmann, R., Mohamed, A., Samejima, H. & Wilting, A. (2013) Risky business or simple solution – relative abundance indices from camera-trapping. *Biological Conservation*, **159**, 405–412.

Stevens, T.H., More, T.A. & Glass, R.J. (1994) Public attitudes about coyotes in New England. *Society & Natural Resources*, **7**, 57–66.

Sturtz, S., Ligges, U. & Gelman, A. (2005) R2WinBUGS: a package for running WinBUGS from R. *Journal of Statistical Software*, **12**, 1–16.

Tablado, Z. & Jenni, L. (2015) Determinants of uncertainty in wildlife responses to human disturbance. *Biological Reviews of the Cambridge Philosophical Society*, doi: 10.1111/brv.12224.

Virginia Department of Game and Inland Fisheries (2012) 2011-2012 Hunter survey report.

Vogt, P., Ritters, K.H., Estreguil, C., Kozak, J., Wade, T.G. & Wickham, J.D. (2007) Mapping spatial patterns with morphological image processing. *Landscape Ecology*, **22**, 171–177.

Vucetich, J.A., Smith, D.W. & Stahler, D.R. (2005) Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. *Oikos*, **111**, 259–270.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Annual harvest estimates showing the relative intensity of hunting across species.

Table S1. List of protected areas surveyed and their characteristics.

Table S2. Complete list of covariates initially considered in VF and occupancy analyses.

Table S3. Full results for occupancy model selection.

Table S4. Model averaged occupancy coefficient estimates for predator species.

Table S5. Model averaged occupancy coefficient estimates for non-predator species.

Table S6. Model averaged occupancy variable importance weights for all species.

Table S7. Full VF model results for each species.

Table S8. Model weights for variable used in full multivariate occupancy models for 12 species.

Table S9. Global model VF coefficient estimates for predator species.

Table S10. Global model VF coefficient estimates for non-predator species.

Table S11. Significant positive (+) or negative (-) relationships between wildlife, housing density, and large core forests from occupancy models accounting for an interaction between the two covariates.