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Caching behaviour by red squirrels may contribute to food conditioning of grizzly bears

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Abstract

We describe an interspecific relationship wherein grizzly bears (*Ursus arctos horribilis*) appear to seek out and consume agricultural seeds concentrated in the middens of red squirrels (*Tamiasciurus hudsonicus*), which had collected and cached spilled grain from a railway. We studied this interaction by estimating squirrel density, midden density and contents, and bear activity along paired transects that were near (within 50 m) or far (200 m) from the railway. Relative to far ones, near transects had 2.4 times more squirrel sightings, but similar numbers of squirrel middens. Among 15 middens in which agricultural products were found, 14 were near the rail and 4 subsequently exhibited evidence of bear digging. Remote cameras confirmed the presence of squirrels on the rail and bears excavating middens. We speculate that obtaining grain from squirrel middens encourages bears to seek grain on the railway, potentially contributing to their rising risk of collisions with trains.

Keywords

Ursus arctos, *Tamiasciurus hudsonicus*, cache pilferage, food conditioning, caching behaviour

Introduction

As an alternative to foraging independently, many animals steal food from other individuals. This behaviour is widespread in birds and mammals, can occur within and among species, and includes the active pursuit of prey-carrying individuals as well as the pilfering of resources from hoards or caches. Such strategies may be occasional and opportunistic, such as for the kleptoparasitism exhibited by several gull species (*Larus* spp.; Brockmann and Barnard 1979, Giraldeau and Beauchamp 1999), and the reciprocal pilfering of caches that occur in several species of small mammals (Vander Wall and Jenkins 2003). These strategies can also occur as a prevalent form of foraging, as in magnificent frigatebirds (*Fregata magnificens*; Gilardi 1994, Vickery and De L Brooke 1994) or via specialization by some individuals, such as that which occurs in house sparrows (*Passer domesticus*; Barnard and Sibly 1981). Pilfering species often have size, mobility, or numerical advantages relative to the individuals that provide the food, including when wolves (*Canis lupus*) steal carcasses from solitary cougars (*Felis concolor*; Kortello et al. 2007). Host species often exhibit counter strategies to deter thieves, which include defence by red squirrels (Gerhardt 2005), scatter hoarding by western scrub-jays (*Aphelocoma californica*; Dally et al. 2006) and use of hiding material by cougars (Beier et al. 1995).

Inter-specific opportunities to steal food create the potential for food conditioning, which is defined simply as the capacity to associate food with another species (Mattson et al. 1992). Food conditioning of wildlife by people contributes to human-wildlife conflict all over the world (reviewed by Donaldson et al. 2012), especially in urban areas (Gehrt 2004). Bears (*Ursus* spp.) are particularly prone to food conditioning (Hopkins et al. 2012), which also makes them more likely to exhibit conflict behaviour (Hopkins et al. 2014a). Experience-based knowledge of this association by wildlife managers is the reason that preventing food conditioning has become a mainstay of wildlife management in protected areas (Herrero 1970, McCullough 1982).

Preventing food conditioning is especially difficult for anthropogenic products that are dispersed in time and space via sources that are ubiquitous and difficult to contain. One such situation is the deposition of agricultural products spilled by trains in the mountain parks of Canada which likely contributes to attraction and associated mortality of grizzly bears on the railway (Bertch and Gibeau 2010, Gangadharan et al. 2017). Wheat (*Triticum* spp.) and other agricultural seeds spill from the bottom-emptying hopper cars, which are prone to slow leaks and occasional larger spills (Dorsey 2011, Shepherd 2014). For this reason, Canadian Pacific, which owns the railway through Banff National Park, avoids siding trains in the park overnight and attempts to remove agricultural seed spills before they can attract bears and other wildlife (K. Roberge, personal communication).

Here we explore the possibility that red squirrels contribute to the targeting of bears to agricultural seeds on the railway, where they are at risk of being hit by passing trains, by conditioning them to agricultural seeds in concentrated caches in their middens. Our work was prompted by the discovery in fall 2013 of a squirrel midden containing agricultural seeds that was visited by a GPS-collared bear (S. Fassina and S. Pollock, personal communication). Although grizzly bears were already known to excavate red squirrel middens to consume the seeds of whitebark pine (*Pinus albicaulis*; Mattson and Reinhart 1997, Hamer and Pengelley 2015), we could find no reference in the literature to bears targeting any other food source in squirrel middens. Red squirrels are active year-round (Gurnell 1984), whereas grizzly bears in this area typically enter partial hibernation between November and March (Graham and Stenhouse 2014). The objectives of this study were to determine if (a) red squirrels occur at higher densities within 50 m of the railway than far from it (~200 m), (b) near middens contain agricultural seeds more often than far ones, and (c) bears visit and excavate middens to consume agricultural seeds. We based our transect positions on expectations that squirrels would collect food items mainly within a close vicinity (<50 m) of their middens (Hurly and Robertson 1987), and would be unlikely to occupy territories with radii of more than 100 m (Rusch and Reeder 1978).

Methods

The study was conducted in Banff (6,836 km²) and Yoho (1,313 km²) National Parks in Canada, along the 134 km section of the Canadian Pacific Railway that runs through the valley bottom (Figure 1A). The railway track within the parks runs from the western border of Yoho National Park (51°14'N, 116°39'W) to the eastern border of Banff National Park (51°8'N, 115°25'W). Common tree species in the study area were lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*) and trembling aspen (*Populus tremuloides*). Whitebark pine occurs in our study area, but it is rare and typically is found only at high altitudes (Hamer and Pengelley 2015, Hamer 2017).

We selected 14 sites (11 in Banff and 3 in Yoho National Parks) at which we positioned paired transects of 500 m that were near the railway (15 m from the forest edge within forest cover, and a maximum of 50 m from the railway) and far from it (200 m from the railway within forest cover). Additionally, these 14 sites were chosen to exhibit continuous forest cover and to differ by less than 100 m in altitude between the pairs of transects. When necessitated by breaks in forest cover, the transect was broken into segments of forest-covered areas that summed to 500 m. For each transect, a predetermined route was followed using a hand-held global positioning system (GPS) unit.

On sunny days between August 12th to 28th 2014, we searched for and recorded squirrel activity within 10 m of the transect line, and recorded individuals and signs of both squirrels and bears. This created an area of 1 ha (20 × 500 m) that we searched for a 1 to 2 hour period. For squirrels, within 10 m of the transect line, we recorded visual sightings, acoustic detections, active primary middens, secondary middens and inactive (old) primary middens. We distinguished active from inactive middens by

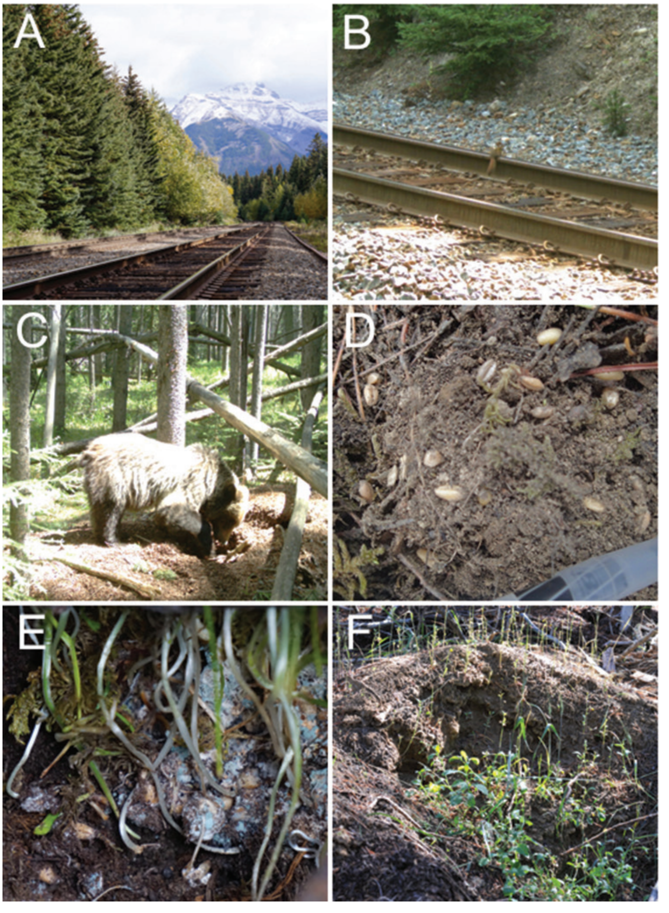

Figure 1. Evidence of bears interacting with squirrel middens for access to agricultural seeds. **A** Railway in Banff National Park, where agricultural seeds are found on the tracks. **B** American red squirrel on the railway, taken with a remote camera on time-lapse settings **C** Grizzly bear excavating a squirrel midden where bear signs were previously recorded during a survey of an area with high bear use. The photo was taken with a remote camera on hyperfire settings **D** Unsprouted agricultural seeds, visibly wheat and lentil, found at an active midden near the railway that had been recently excavated **E** Moldy sprouted and unsprouted agricultural seeds, visibly chickpeas, wheat, flax, lentils and canola, at an excavated inactive primary midden near the railway **F** Sprouted agricultural plants at an inactive primary midden near the railway.

squirrel occupation (i.e. observed squirrel at midden, freshly clipped pine cones and/or fresh squirrel digging), and primary from secondary middens by size (>4m^2 vs <1m^2, respectively). For bears, we recorded evidence of bedding, digging, rubbed trees, claw scratching on trees, digging for ants (in the ground or logs), berry feeding, herbaceous feeding and presence of scat if they occurred within 5 m of a primary midden. If scat was found, we visually inspected it for cone bracts and needles (of pine or spruce) and agricultural seeds. At the start, middle, and end points of each transect, we recorded forest type and canopy cover. The forest type was quantified by the dominant species in a count of trunks with a diameter at breast height (dbh) greater than 10 cm that were within 25 m of the plot centroid. We used a concave densiometer to quantify canopy cover. Both canopy cover and tree species are known to be predictors of squirrel density (Gurnell 1984). During data collection, the first author was responsible for searching for squirrel and bear signs, and measuring forest type and canopy cover, while a second observer was responsible for recording observations.

To confirm the presence of bears at middens and squirrels on the railway, we installed remote cameras (PC800 and PC900, RECONYX, Holmen, WI, USA) at 12 primary middens near the railway that had high rates of squirrel activity and nearby locations on the railway with a goal of confirming bear visitation to middens and squirrel visitation to the railway.

From October 8th to 21st 2014, we revisited the active primary middens we found during our first visit to sample them for agricultural seeds and record new bear activity associated with them. During this period there was not yet snow on the ground and we expected that squirrels would have completed caching cones, but bears would not yet be in hibernation (Kendall 1983). First, we recorded any new bear activity associated with the midden. Then, we used a post-hole digger (⌀=10 cm) to sample the contents up to 20 cm deep in middens by collecting five samples from small middens (4–20 m^2), 10 samples from medium-sized middens (21–40 m^2) and 15 samples from large middens (41–60 m^2). Samples were taken from areas of the midden that contained the highest level of hoarding activity, categorized by large piles of stored food items, and areas of the midden that had recent squirrel digging. When possible, even numbers of samples were taken from areas with and without evidence of recent squirrel digging. We recorded the number of midden samples with agricultural seeds, as well as the type of seeds found in each midden. During this second visit, we went back to the sites in approximately the same order as the first visit, to maintain consistent time between visits. We placed each midden sample on a bright blue corrugated plastic board, and then systematically examined small subsets of the sample for grain presence until the whole sample had been visually examined. The blue colour of the board contrasted with the midden contents, so the contents within the sample were more easily distinguishable. We recorded the number of samples from a midden that contained grain, as well as grain type.

We revisited the active primary middens for a third time from September 18th to 20th 2015 to record new bear signs. During this visit, we also measured altitude at three points along the railway at each site, at approximately parallel locations to the start, middle and end points of the transects. Altitude was measured for its potential effect on food availability for squirrels and bears.

To overcome potential differences in our ability to detect active primary middens with increasing distance from the transect line, we fitted detection functions. During the first visit, a GPS point was taken at the edge of each midden closest to the transect line. We calculated the distance of the primary middens from transect line in ArcGIS 10.3.1 (ESRI 2015). Using the Distance package (Miller 2016) in R (version 3.2.3, R Core Development Team, Boston, MA, USA), we fit a detection function of the midden locations from the transect lines, and calculated the goodness-of-fit.

For the statistical analysis, we assessed the significance of each predictor variable alone and each combination of two predictor variables in a series of models for each response variable. In models with two predictor variables, we added an interaction term. To assess the significance of models in relation to one another, we used corrected Akaike's Information Criterion (AIC_C) values and average coefficients of the models. For each model set, we performed an analysis of variance (ANOVA) between the model with the lowest AIC_C value to the null model. Each model series used one response variable, these were squirrel sightings, active primary midden density, all (active and inactive) primary midden density, secondary midden density, agricultural seeds in middens, and bear digging in middens. In each series of models, transect location (near or far) was included as one of the predictor variables. Variance inflation factors (VIF) were used to test if there were correlated predictor variables (VIF > 5).

For squirrel sightings, active primary midden density, all primary midden density and secondary midden density, we used multiple generalized linear mixed models (GLMM), with site as a random effect. The squirrel sightings and active primary midden density were run with a poisson distribution, all primary midden density with a negative binomial distribution and secondary middens with a normal distribution. To obtain normally distributed residuals, we transformed the secondary midden counts by taking the natural log. For squirrel sightings and primary midden density, we included transect location, canopy cover and altitude as potential predictor variables. Visual squirrel sightings were only used for squirrel detections, owing to their correlation with acoustic detections (Kendall's tau = 0.42, P = 0.014). Red squirrels are common and have high detectability, so false zeros for visual sightings would likely be due to the shortness of the survey period relative to their temporary absence during home-range movements (Dénes et al. 2015). For secondary middens, we used size of active primary middens, as well as transect location, canopy cover and altitude.

For agricultural seed presence and bear digging in middens, we used a logistic regression. For agricultural seeds in middens, the potential predictor variables included in the models were transect location, canopy cover and altitude. For bear digging in middens, transect location, the proportion of samples with agricultural seeds detected and altitude were used as potential predictor variables. All analyses were performed in R using the packages Distance (Miller 2016), glmmADMB (Skaug et al. 2015) and lme4 (Bates et al. 2015).

Results

Among the 14 pairs of transects parallel to the railway, we detected a total of 221 primary middens and 9566 secondary middens with similar densities near and far from the rail (Table 1). Size of active primary middens and altitude with their interaction best predicted the number of secondary middens detected ($\chi^2 = 21.9$, df = 3, P < 0.001). Despite a trend toward higher prevalence near the railway (Table 1), active primary middens were best predicted by their positive relationship with forest cover

Table 1. Mean ± SD of squirrel sightings, middens, midden samples containing agricultural products, middens with evidence of bear activity, and forest cover measured on 14 pairs of 500 m transects positioned near (< 50 m) and far (≈ 200 m) from the rail in Banff and Yoho National Parks in 2014. The differences between transect means are reported as ([near – far] / far * 100) with their significance assessed via generalized linear models using the best-fitting distribution with transect location as the single predictor variable.

Variable		Transect (Mean ± SD)		Difference (%)	χ^2	P
		Near	Far			
Squirrel density (per ha)	Sightings	1.86 ± 1.29	0.79 ± 0.80	135.4	6.26	0.012
Midden density (per ha)	Primary	8.78 ± 5.83	7.00 ± 6.11	25.4	2.83	0.432
	Primary - Active	1.71 ± 1.54	1.29 ± 1.20	32.6	0.86	0.408
	Primary - Inactive	7.07 ± 5.20	5.71 ± 5.90	23.8	2.02	0.523
	Secondary	394.21 ± 812.85	288.86 ± 546.79	36.5	1.81	0.36
Agricultural seeds in middens	Proportion of middens with seeds	0.58 ± 0.50	0.06 ± 0.24	866.7	14.42	<0.001
	Proportion of samples / midden with seeds	0.19 ± 0.23	0.02 ± 0.09	850	28.49	0.003
Bear activity at middens	All signs	0.29 ± 0.46	0.06 ± 0.24	383.3	4.2	0.04
	Digging	0.21 ± 0.41	0.00 ± 0.00	NA	6.1	0.014
	Digging and agricultural seeds	0.17 ± 0.38	0.00 ± 0.00	NA	4.79	0.029
	Bedding	0.00 ± 0.00	0.06 ± 0.24	NA	1.73	0.189
	Digging at inactive middens	0.09 ± 0.29	0.01 ± 0.11	800	6.06	0.014
Ecological variables	Forest cover	68.21 ± 12.1	71.96 ± 9.04	-5.2	98.75	0.354

(χ^2 = 10.1, df = 1, P = 0.002), whereas the sum of active and inactive primary middens was best predicted by the combination of forest cover and transect location (χ^2 = 10.1, df = 2, P = 0.006). Our overall ability to detect primary middens was very high (0.99 ± 0.16) with no evidence that detectability was affected by distance to the transect line (Kolmogorov-Smirnov test, χ^2 = 0.13, P = 0.477). Consequently, we did not include detectability in our model of midden abundance. Squirrel sightings were more prevalent near the railway (135.4% higher; Table 1), and best predicted by the combination of transect location and altitude (χ^2 = 11.9, df = 2, P = 0.003).

Of the 15 middens in which we detected one or more types of agricultural seeds or their sprouted plants, 14 were on transects near the railway and only 1 was located far from the railway (Table 1). The best predictors of agricultural seed presence in middens was transect location and forest cover (χ^2 = 16.9, df = 2, p < 0.001). These middens revealed a wide variety of seed types, primarily canola (*Brassica* spp.) and wheat (*Triticum aestivum*), but also including sprouted wheat, soybean (*Glycine max*), canary seed (*Phalaris canariensis*) and sulfur pellets. Agricultural seeds were found in 18.6% of midden samples (n = 180) near the railway, and only 2.2% of midden samples (n = 135) far from the railway.

We detected evidence of bear activity at seven active middens in 2014, six of which were on transects near the railway (Table 1; for video evidence see Suppl. material 1).

Of the active middens near the railway with bear signs of any sort, five showed evidence of bear digging, which reached up to 1m in depth (Figure 1C). Four of these middens contained agricultural products when the midden samples were taken (Figure 1D). The midden near the railway with non-digging bear signs exhibited a bear scat on its surface containing wheat and sulfur pellets. The single active midden with bear signs far from the railway was a bedding site, and no agricultural seeds were observed. The proportion of samples with agricultural seeds in middens and transect location best predicted digging by bears (χ^2 = 10.7, df = 2, P = 0.005). Remote cameras at squirrel middens confirmed that grizzly bears excavated the middens (see video in Suppl. material 1). When we revisited previously active middens in 2015, we found evidence of bear activity at two middens, one near the railway (where there was digging and sprouted canola) and one far from the railway (which had been used for bedding).

Discussion

The purpose of this study was to determine whether caching of agricultural seeds by red squirrels could potentially contribute, via food conditioning, to the risk of train strikes on grizzly bears foraging for spilled grain on a railway. Our results suggest it might. Red squirrels were 2.4 times more prevalent near than far from the railway, and 14 of the 15 middens where we detected agricultural seeds were located on the near transects. Squirrels on the railway were observed harvesting grain, and we recorded digging by grizzly bears only at middens near the railway where they appeared to target agricultural seeds.

The higher density of red squirrels visually detected near the railway was likely caused by the food supplement afforded by spilled agricultural seeds. Caching behaviour is generally responsive to habitat conditions (Dally et al. 2004, Tsurim and Abramsky 2004), and supplemental food typically results in an increase in population density (Boutin 1990). Supplemental food can increase the density of red squirrels by 3-4 times, in turn, increasing recruitment (Sullivan 1990). Unlike squirrel sightings, primary midden density was not statistically different between the transect locations. An explanation for this could be that the transect area near the railway was closer to the forest edge than where high densities of primary middens occurred. In our study, secondary middens were 36% more prevalent near than far from the railway, which might have been an adaptation to reduce losses to pilfering by bears or conspecifics, or a response to greater food availability. Smaller caches and scatter-hoarding appear to reduce the rate of pilfering in both birds (Brodin and Ekman 1994) and mammals (Daly et al. 1992, Geluso 2005). Previous studies have found scatter-hoarding rodents, including squirrels, also maintain smaller caches when food is more abundant (Moore et al. 2007), which was not supported in our study.

We observed that agricultural seeds were collected from the railway by red squirrels, and we detected them considerably more often in middens that were near the railway (Figure 1B). Scatter-hoarding rodents preferentially cache valuable food items and transport them farther distances than items of lesser value (Moore et al. 2007). Although red squirrels typically collect items within 10 m of their middens (Hurly and Lourie 1997), the distance between the railway and middens in the near transect was an average of 39.1 m. The single midden that was 200 m from the railway with agricultural seeds may have resulted from intraspecific pilfering.

The fact that we observed digging by grizzly bears in middens only near the railway and almost exclusively where we also detected agricultural seeds suggests that bears smell the seeds and target seed-containing middens. The digging signs we observed were consistent with a targeted search, although at least one observation on transects and several incidentally while doing field work suggest that bears also use middens as bed sites. We found no evidence that bears were affected by the remote cameras set up at middens near the railway, such as photos of bears approaching or manipulating the cameras. Bears are notoriously opportunistic in their foraging habits (Gunther et al. 2014) and quickly adapt to target more abundant resources (Hopkins et al. 2014b), particularly when traditional food sources are rare (Fortin et al. 2013). In our study area, bears rely extensively on Canada buffaloberry (*Shepherdia canadensis*), which exhibits large inter-annual variation in productivity (Hamer and Herrero 1987). Because our data were collected mainly in 2014, which was a particularly poor berry year (Pollock et al., *in review*), bear use of middens may have been unusually high.

Additional evidence suggests that excavating squirrel middens may be a widespread behaviour by bears in this region and potentially other ones. A larger concurrent project, of which this study was a part, recorded extensive use of the forested areas near (< 1000 m) the rail by grizzly bears wearing GPS collars. Site investigations at locations with multiple fixes, detected excavated squirrel middens at 12 / 58 (21%) of these locations in 2014 and 4 / 31 (13%) in 2015, in total representing at least 9 individual bears (unpublished data). The excavated sites were attributed to 9 / 19 (47%) of the collared bears in the study area. Our remote cameras (which were not set up at all middens), captured photos of 2 different grizzly bears (one collared and one uncollared) digging into different middens. Bears in our study area also excavate middens at higher altitudes to obtain whitebark pine seeds (Hamer and Pengelley 2015, Hamer 2017), and that behaviour might easily facilitate foraging at lower altitudes for agricultural seeds. However, it seems likely that there are individual behavioural differences among bears in the region which could vary the degree to which they are food conditioned to consuming grain in squirrel middens.

Our study has identified several topics that could be investigated in future studies. One goal could be to determine whether black bears (*Ursus americanus*) contributed to some of the digging we observed, although this species is less adapted to digging than grizzly bears (Mattson and Reinhart 1997). Another possibility is that bears digging in middens were attempting to catch squirrels or small rodents that might try to pilfer from them, or other available food items. Grizzly bears routinely dig for Columbian ground squirrels (*Urocitellus columbianus*; Munro et al. 2006), and we observed many bear digging sites along the railway in association with ground squirrel burrows. Equal focus could be applied to active and inactive middens, as we observed bear digging at inactive middens with agricultural products visible during our first visit and through incidental observations (Figure 1E–F). Further investigations could also quantify the potential food value and volume of agricultural seeds obtained by bears from squirrel middens.

Conclusions

In summary, we have shown red squirrels frequent the railway, occur at higher densities along it, and cache several kinds of spilled agricultural seeds in their middens. We documented excavations of squirrel middens by grizzly bears that appear to be targeting agricultural seeds and comparable behaviour was evident in half of the collared bears in our study area. Together, these results suggest that squirrels may contribute, via food conditioning, to the tendency for bears to target grain on the railway, which may subsequently increase their risk of being struck by trains. In addition to conditioning bears to target grain, the caching of agricultural seeds by red squirrels, as well as their consumption by bears and other species, may cause the spread of these agricultural species in Banff and Yoho National Parks. Our study exemplifies the complexity of both food conditioning and vulnerability to train strikes associated with spilled agricultural products on railways. The only feasible mitigation for these effects is likely to reduce spillage from hopper cars via careful attention to loading and gate maintenance.

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References

Barnard CJ, Sibly RM (1981) Producers and scroungers: a general model and its application to captive flocks of house sparrows. Animal Behaviour 29: 543–550. https://doi.org/10.1016/S0003-3472(81)80117-0

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48. https://doi.org/10.18637/jss.v067.i01

Beier P, Choate D, Barrett RH (1995) Movement patterns of mountain lions during different behaviors. Journal of Mammalogy 76: 1056–1070. https://doi.org/10.2307/1382599

Bertch B, Gibeau ML (2010) Grizzly bear monitoring in and around mountain national parks: mortalities and bear-human encounters 1980–2009. Third annual report, March 2010. Parks Canada Agency, Lake Louise.

Boutin S (1990) Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Canadian Journal of Zoology 68: 203–220. https://doi.org/10.1139/z90-031

Brockmann HJ, Barnard CJ (1979) Kleptoparasitism in birds. Animal Behaviour 27: 487–514. https://doi.org/10.1016/0003-3472(79)90185-4

Brodin A, Ekman J (1994) Benefits of food hoarding. Nature 372: 510–510. https://doi.org/10.1038/372510a0

Dally JM, Emery NJ, Clayton NS (2004) Cache protection strategies by western scrub-jays (*Aphelocoma californica*): hiding food in the shade. Proceedings of the Royal Society B: Biological Sciences 271: S387–S390. https://doi.org/10.1098/rsbl.2004.0190

Dally JM, Emery NJ, Clayton NS (2006) Food-caching western scrub-jays keep track of who was watching when. Science 312: 1662–1665. https://doi.org/10.1126/science.1126539

Daly M, Jacobs LF, Wilson MI, Behrends PR (1992) Scatter hoarding by kangaroo rats (*Dipodomys merriami*) and pilferage from their caches. Behavioral Ecology 3: 102–111. https://doi.org/10.1093/beheco/3.2.102

Dénes FV, Silveira LF, Beissinger SR (2015) Estimating abundance of unmarked animal populations: accounting for imperfect detection and other sources of zero inflation. Methods in Ecology and Evolution 6: 543–556. https://doi.org/10.1111/2041-210X.12333

Donaldson R, Finn H, Bejder L, Lusseau D, Calver M (2012) The social side of human-wildlife interaction: wildlife can learn harmful behaviours from each other. Animal Conservation 15: 427–435. https://doi.org/10.1111/j.1469-1795.2012.00548.x

Dorsey B (2011) Factors affecting bear and ungulate mortalities along the Canadian Pacific railroad through Banff and Yoho National Parks. MSC Thesis. Montana State University (Bozeman). http://scholarworks.montana.edu/xmlui/handle/1/1190

Fortin JK, Schwartz CC, Gunther KA, Teisberg JE, Haroldson MA, Evans MA, Robbins CT (2013) Dietary adjustability of grizzly bears and American black bears in Yellowstone National Park. The Journal of Wildlife Management 77: 270–281. https://doi.org/10.1002/jwmg.483

Gangadharan A, Pollock S, Gilhooly P, Friesen A, Dorsey B, St. Clair CC (2017) Grain spilled from moving trains create a substantial wildlife attractant in protected areas. Animal Conservation. https://doi.org/10.1111/acv.12336

Gehrt S (2004) Ecology and management of striped skunks, raccoons, and coyotes in urban landscapes. In: Fascione N, Delach A, Smith ME (Eds) People and Predators: From Conflict To Coexistence. 2nd edition. Island Press, Washington, 81–104. https://islandpress.org/book/people-and-predators

Geluso K (2005) Benefits of small-sized caches for scatter-hoarding rodents: influence of cache size, depth, and soil moisture. Journal of Mammalogy 86: 1186–1192. https://doi.org/10.1644/05-MAMM-A-016R1.1

Gerhardt F (2005) Food pilfering in larder-hoarding red squirrels (*Tamiasciurus hudsonicus*). Journal of Mammalogy 86: 108–114. https://doi.org/10.1644/1545-1542(2005)086<0108:FPILRS>2.0.CO;2

Gilardi JD (1994) Great frigatebird kleptoparasitism: sex-specific host choice and age-related proficiency. The Condor 96: 987–993. https://doi.org/10.2307/1369107

Giraldeau LA, Beauchamp G (1999) Food exploitation: searching for the optimal joining policy. Trends in Ecology and Evolution 14: 102–106. https://doi.org/10.1016/S0169-5347(98)01542-0

Graham K, Stenhouse GB (2014) Home range, movements, and denning chronology of the grizzly bear (*Ursus arctos*) in west-central Alberta. Canadian Field-Naturalist 128: 223–234. https://doi.org/10.22621/cfn.v128i3.1600

Gunther KA, Shoemaker RR, Frey KL, Haroldson MA, Cain SL, van Manen FT, Fortin JK (2014) Dietary breadth of grizzly bears in the Greater Yellowstone ecosystem. Ursus 25: 60–72. https://doi.org/10.2192/URSUS-D-13-00008.1

Gurnell J (1984) Home range, territoriality, caching behaviour and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in a subalpine lodgepole pine forest. Animal Behaviour 32: 1119–1131. https://doi.org/10.1016/S0003-3472(84)80228-6

Hamer D (2017) Excavation of red squirrel (Tamiasciurus hudsonicus) middens by bears (Ursus spp.) in limber pine (Pinus flexilis) habitat in Banff National Park, Alberta. Canadian Field-Naturalist 130: 281–288. https://doi.org/10.22621/cfn.v130i4.1918

Hamer D, Herrero S (1987) Grizzly bear food and habitat in the front ranges of Banff National Park, Alberta. Bears: Their Biology and Management 7: 199–213. https://doi.org/10.2307/3872626

Hamer D, Pengelley I (2015) Whitebark pine (*Pinus albicaulis*) seeds as food for bears (*Ursus* spp.) in Banff National Park, Alberta. Canadian Field-Naturalist 129: 8–14. https://doi.org/10.22621/cfn.v129i1.1662

Herrero S (1970) Human injury inflicted by grizzly bears. Science 170: 593–598. https://doi.org/10.1126/science.170.3958.593

Hopkins JB, Koch PL, Ferguson JM, Kalinowski ST (2014a) The changing anthropogenic diets of American black bears over the past century in Yosemite National Park. Frontiers in Ecology and the Environment 12: 107–114. https://doi.org/10.1890/130276

Hopkins JB, Koch PL, Schwartz CC, Ferguson JM, Greenleaf SS, Kalinowski ST (2012) Stable isotopes to detect food-conditioned bears and to evaluate human-bear management. Journal of Wildlife Management 76: 703–713. https://doi.org/10.1002/jwmg.318

Hopkins JB, Whittington J, Clevenger AP, Sawaya MA, St. Clair CC (2014b) Stable isotopes reveal rail-associated behavior in a threatened carnivore. Isotopes in Environmental and Health Studies 50: 322–331. https://doi.org/10.1080/10256016.2014.922555

Hurly TA, Lourie SA (1997) Scatterhoarding and larderhoarding by red squirrels: size, dispersion, and allocation of hoards. Journal of Mammalogy 78: 529–537. https://doi.org/10.2307/1382904

Hurly TA, Robertson RJ (1987) Scatterhoarding by territorial red squirrels: a test of the optimal density model. Canadian Journal of Zoology 65: 1247–1252. https://doi.org/10.1139/z87-194

Kortello AD, Hurd TE, Murray DL (2007) Interactions between cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff National Park, Alberta. Ecoscience 14: 214–222. https://doi.org/10.2980/1195-6860(2007)14[214:IBCPCA]2.0.CO;2

Mattson D, Blanchard B, Knight R (1992) Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. The Journal of Wildlife Management 56: 432–442. https://doi.org/10.2307/3808855

Mattson D, Reinhart D (1997) Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. Journal of Applied Ecology 34: 926–940. https://doi.org/10.2307/2405283

McCullough D (1982) Behavior, bears, and humans. Wildlife Society Bulletin 10: 27–33. https://www.jstor.org/stable/3781798?seq=1#page_scan_tab_contents

Miller DL (2016) Distance: Distance Sampling Detection Function and Abundance Estimation. R package version 0.9.6. https://CRAN.R-project.org/package=Distance

Moore JE, McEuen AB, Swihart RK, Contreras TA, Steele MA (2007) Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. Ecology 88: 2529–2540. https://doi.org/10.1890/07-0247.1

Munro R, Nielsen S, Price M, Stenhouse G, Boyce M (2006) Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. Journal of Mammalogy 87: 1112–1121. https://doi.org/10.1644/05-MAMM-A-410R3.1

R Development Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Austria. www.R-project.org

Rusch D, Reeder W (1978) Population ecology of Alberta red squirrels. Ecology 59: 400–420. https://doi.org/10.2307/1936382

Shepherd B (2014) Grain spill trend on the railway tracks in Jasper National Park: 2008-2012. Parks Canada Agency, Jasper.

Skaug H, Fournier D, Bolker B, Magnusson A, Nielsen A (2015) Generalized linear mixed models using "AD Model Builder." R package version 0.8.3.2. https://rdrr.io/rforge/glmmADMB/

Sullivan TP (1990) Responses of red squirrel (*Tamiasciurus hudsonicus*) populations to supplemental food. Journal of Mammalogy 71: 579–590. https://doi.org/10.2307/1381797

Tsurim I, Abramsky Z (2004) The effect of travel costs on food hoarding in gerbils. Journal of Mammalogy 85: 67–71. https://doi.org/10.1644/1545-1542(2004)085<0067:TEOTCO>2.0.CO;2

Vander Wall SB, Jenkins SH (2003) Reciprocal pilferage and the evolution of food-hoarding behavior. Behavioral Ecology 14: 656–667. https://doi.org/10.1093/beheco/arg064

Vickery JA, Brooke M (1994) The kleptoparasitic interactions between great frigatebirds and masked boobies on Henderson Island, South Pacific. The Condor 96: 331–340. https://doi.org/10.2307/1369318

Supplementary material 1

Video of grizzly bear digging into a red squirrel midden

Authors: Julia Elizabeth Put, Laurens Put, Author, Colleen Cassady St. Clair

Data type: MPG video file

Link: https://doi.org/10.3897/natureconservation.21.12429.suppl1

Supplementary material 2

Data collected along transects

Authors: Julia Elizabeth Put, Laurens Put, Author, Colleen Cassady St. Clair

Data type: specimens data

Link: https://doi.org/10.3897/natureconservation.21.12429.suppl2

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RESEARCH ARTICLE

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Herpetofauna inside and outside from a natural protected area: the case of Reserva Estatal de la Biósfera Sierra San Juan, Nayarit, Mexico

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Abstract

Natural Protected Areas (NPAs) includes important species richness, and it is assumed that these are the best areas for biodiversity conservation. There are certain doubts, however, about the effectiveness of the NPAs in developing countries, where economic resources for conservation are scarce and NPAs are not monitored and managed efficiently. In the present study we assessed the species richness, diversity, abundance, and functional guilds of amphibians and reptiles inside and outside of the NPA Reserva Estatal de la Biósfera Sierra San Juan (REBSSJ), Nayarit, Mexico. Our results showed that species numbers of amphibian and reptiles were higher outside than inside the reserve, as well the individual number distributed among species, except for lizard species. Analyses of functional guilds showed that both richness and functional dispersion were greater in amphibians and reptiles outside the reserve. Likewise, outside the reserve we recorded a higher species number with some category of risk at the national level (NOM-059), international level (IUCN), and also by using the Environmental Vulnerability Score (EVS) algorithm. The results suggest that areas outside of the reserve are crucial to the maintenance of regional biodiversity, due to high complementarity with species composition inside of the reserves. These data can be used to implement conservation measures that include a new demarcation of the reserve and the consideration of surrounding areas to include a great number of species.

Keywords
Amphibians, abundance, conservation, diversity, natural protected area, reptiles

Introduction

Worldwide, the creation of Natural Protected Areas (NPAs) has been one of the major measures to conserve biodiversity (Rodrigues et al. 2004). Under certain scenarios, however, it has been found that parks may not be the optimal governance structure for promoting local conservation, primarily because economic and human resources are scarce (Hayes 2006) and such areas become only paper parks (Rife et al. 2013, Blackman et al. 2015). Mexico has 182 NPAs decreed under different categories, such as national parks, biosphere reserves, and natural monuments, among others (CONANP 2017).

In spite of the high number of NPAs registered currently, most of them have been established in an arbitrary way, because in most cases there is a lack of basic biological information of the species that are in these areas (Ervin 2003). As such, it is important to assess the efficiency of the decreed NPAs, because in most cases not all components of the biodiversity are preserved, e.g., species, vegetation types, ecosystems, homogeneity, and heterogeneity (Chape et al. 2005). On the other hand, these areas are damaged by anthropic effects, such as illegal looting of flora and fauna, pollution, deforestation, landscape fragmentation, and land-use change (Ervin 2003, Figueroa and Sánchez-Cordero 2008). This disturbance has been consistently evident in tropical areas of developing countries (Román-Cuesta and Martínez-Villalta 2006, Urbina-Cardona et al. 2006). For example, in Sierra San Juan, in Nayarit, Mexico there is a Reserva Estatal de la Biosfera Sierra San Juan (REBSSJ), which was declared in 1987 with the objective to stop the exploitation of banks of materials (González 2010). At the time of being declared as an NPA, however, government officials did not have available accurate information on diversity and abundance of the species, as well as the values of elements of biodiversity of landscape or the most outstanding natural processes; instead, it used as a criterion for its delimitation surface which is comprised up of 980 m a.s.l. (González 2010).

The REBSSJ is located at the westernmost extreme of the Mexican Transvolcanic Belt, in Sierra San Juan, which constitutes a geomorphological unit separated of this biogeographic province (Luhr 2000). Due to this isolation, the study of biological diversity in the REBSSJ is very interesting because it illustrates several vegetation types, which are semi-deciduous tropical forest, cloud forest, oak forest, pine forest, oak-pine forest, and secondary scrubland (Téllez 1995). In this area, there are at least 1250 species of plants and ferns (30% of the flora reported for Nayarit), of which 31 are endemic to Mexico (Téllez 1995), and at least 370 species of birds (44.9% reported from Nayarit; Espinosa 2000).

The amphibians and reptiles from this region have been poorly studied. The only previous study for the site is a catalogue of the species of this group by Bojórquez

(2003). In this work, 36 species were reported from Sierra San Juan and 12 for the REBSSJ. In this catalogue is included the Mexican Spiny-tailed Iguana (*Ctenosaura acanthura*) and Tehuantepec Striped Snake (*Geagras redimitus*). Natural distribution of these species occurs quite far from REBSSJ, because the former species occurs in states bordering the Gulf of Mexico and the latter in the southeastern portion of the country (Ramírez-Bautista and Hernández-Ibarra 2004, Canseco-Márquez 2007); therefore, these two species suggest an erroneous of species identification from REBSSJ. Recently, Woolrich-Piña et al. (2016) published an article on the herpetofauna of Nayarit, in which they included a limited analysis of diversity in NPAs including REBSSJ. This revision was made based on literature reviews and opportunistic fieldwork only, so the authors did not conduct systematic fieldwork and the data presented on this paper concerning the REBSSJ should be taken with caution.

In order to assess the effectiveness of this NPA, the objectives of this study are: (i) to determine species richness, abundance, functional richness, functional equality, and functional dispersion of amphibians and reptiles inside and outside of the REBSSJ, and (ii) to compare diversity patterns inside and outside of the REBSSJ. This work is important because in spite of being a protected area, diverse anthropic activities are conducted within its boundaries, such as coffee and avocado cultivation, without supervised regulation or estimation of the impact on biodiversity. Thus our hypothesis of work is that because the natural protected area is surrounded by zones highly transformed; therefore there will be a different number of species and communities composition of amphibians and reptiles, with low number of species outside of reserve.

Methods

Study Area

The study area is located in Sierra San Juan in the central portion of the state of Nayarit, and comprises part of the municipalities of Tepic, Xalisco, and San Blas (21°20'–21°32'N; 104°53'–105°03'W; datum WGS84; Figure 1). Elevations in the sierra range from 400 to 2250 m. The climate according to Köppen classification, as modified by García (1988), is semi-arid and temperate. A semi-warm climate also exists, at elevations of 1200 m., with a temperature from 18°C to 22°C. On the other hand, temperate regions presents mean annual temperatures from 15.5°C to 18°C at an elevation of 1200 m. Mean annual precipitation varies between 1100 and 1700 mm, which occurs from June to October. Vegetation types of the Sierra San Juan are oak forest, oak-pine forest, and patches of cloud forest (Téllez 1995). Outside of the reserve, vegetation type has been modified by anthropic effects, and it is avocado cultivation (east zone) and mango cultivation (west zone), with patches of semi-deciduous tropical forest, and less extension of cloud forest, which is a strip that is located between 700 and 1200 m of elevation, which is devoted to coffee plantation under shade.

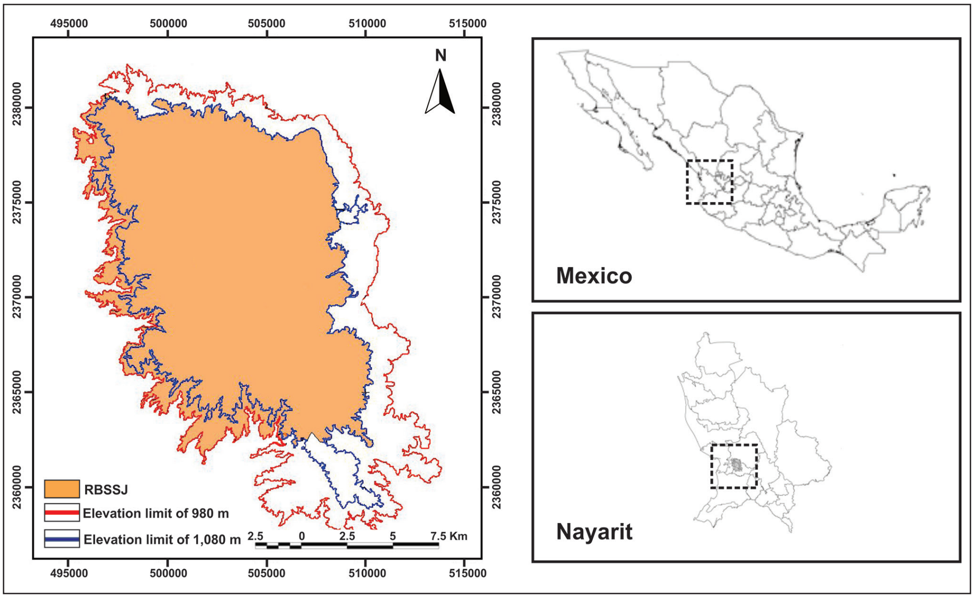

Figure 1. Location of the Reserva Estatal de la Biósfera Sierra de San Juan (REBSSJ) in the Sierra San Juan Nayarit, Mexico. Modified from González (2010).

Fieldwork

This study was carried out between June 2012 and August 2015. Surveys were conducted during each month in a systematic way by dedicating a whole day of sampling for searching the amphibians and reptiles inside and outside of the reserve. For each day, random surveys of the specimens were made by two people, which began from 09:00 to 14:00 h, and from 17:00 to 22:00 h (10 h/man by 2 persons = 20 man hours). Total sampling was an effort of 1520 man-hours equally distributed inside and outside of the reserve (760 h/man each one). Amphibians and reptiles were searched for during the hikes by checking all habitats and microhabitats types, such as under rocks and logs and within litter, holes, and crevices (Casas-Andreu et al. 1991). In order to avoid pseudoreplication we did not sample in the same site more than a single time (Luja et al. 2008). The first five specimens each species observed in the field were collected by hand or herpetological hooks in case of individuals of genus *Crotalus*, to be identified based on our experience or with dichotomous keys, and each specimen was photographed, which photographs were housed at Texas University in Arlington (UTADC). In this study we followed the taxonomy by Wilson et al. (2013a, b).

Data analysis

In order to estimate the completeness of the inventory of the amphibians and reptiles from inside and outside the reserve, we constructed a species accumulation curve

(Moreno 2001) using the program ESTIMATES ver. 750 (Colwell 2005). Because the analysis was performed by using abundance of the species, we used the non-parametric estimators ACE and Chao 1 (Jiménez-Valverde and Hortal 2003); in addition, we used logarithms that assess species that were represented in samples by 1 (singletons) or 2 (doubletons) individuals (Colwell and Coddington 1994).

Species diversity of amphibians and reptiles was assessed inside and outside of the reserve by effective species number according to the method proposed by Jost (2006). For this analysis we took into consideration the order q = 1, it considers proportional abundance of each species (Jost 2006). The equation is represented as $^{1}D = \exp(H')$, where ^{1}D is the true diversity, and exp (H') is the Shannon exponential index (Jost 2006, Moreno et al. 2011). On the other hand, we compared species richness between sites considering the abundance of the individuals by rarefaction curves (Gotelli and Colwell 2001). These curves were generated by the program PAST (Hammer et al. 2001). In addition, to assess the abundance and equity of amphibians and reptiles inside and outside of the reserve we performed curves of rank-abundance (Magurran 1998, Feinsinger 2003) by using species number and individuals per species recorded in the study area. The curves were graphed according to logarithm of proportion of each species p(n/N), and the data is sorted from the most abundant species to the least abundant.

To assess beta diversity between areas we used the complementarity index (Colwell and Coddington 1994). For this analysis we related the number of species of site A to the number of species of site B, and the number of species in common between A and B (Colwell and Coddington 1994). Therefore, in this way we obtained the species richness for both communities by the formula SAB = a + b - c, where a is the species number of the site A, b is the species number of species in the site B, and c is the number of species in common between sites A and B. Exclusive species number (U) for any place is represented as UAB = a + b – 2c, and with these values, the complementarity (C) between both places was calculated as CAB = U AB/SAB. Complementarity values vary from 0 when both places are identical in their composition to 1 when species of both places are different (Colwell and Coddington 1994).

Finally, to assess the functional diversity (FD) we collected information (on literature and databases) about four specific traits: i) Habits (terrestrial, arboreal, terrestrial semi arboreal and terrestrial freshwater), ii) Diet (insects, insects and small mammals, insects and vegetables, small mammals, lizards and rodents, amphibians, small rodents, amphibians and lizards, lizards and snakes, lizards and small mammals, fish and aquatic insects), iii) Activity (diurnal, nocturnal, diurnal and nocturnal), and iv) Foraging mode (active or sit-and-wait). To obtain the values of FD, three measures as response variables were calculated using multivariate methods, one that uses information presence or absence of each species (functional richness, Fr), and two measures that incorporate information on the abundance of species (functional equity, Fe) and functional dispersion (Fd). This method was chosen because functional characterization of the assemblage is achieved by considering jointly these three components (Mason et al. 2005, Villéger et al. 2008), hence its classification as multidimensional indices that are based on the profile of the traits of each species (Laliberté and Legendre 2010). Functional Diversity indices were calculated based on the Gower distance using the software FDIVERSITY (Casanoves et al. 2011).

Results

Herpetofauna from Sierra San Juan

Species composition of the Sierra San Juan is 55 in total. Five families, 10 genera, and 15 species represent amphibians, whereas reptiles are represented by 18 families, 32 genera, and 40 species (Table 1). Among amphibians, the family Hylidae was the most diverse, with 5 species; Craugastoridae contained four species, while Bufonidae, Eleutherodactylidae, and Ranidae each contain two species. Two turtle species are represented by one family each, Geoemydidae and Kinosternidae, and one genus in each (Table 1). Lizard species were represented among eight families, nine genera, and 14 species. The family Phrynosomatidae was represented by six species, Teiidae with two, and the families Anguidae, Dactyloidae, Gekkonidae, Helodermatidae, Iguanidae, and Scincidae were represented by one species each (Table 1). Finally, snake species are represented by eight families and 21 genera, which are Boidae, Colubridae, Dipsadidae, Elapidae, Leptotyphlopidae, Natricidae, Typhlopidae, and Viperidae (Table 1).

Herpetofauna inside REBSSJ

In this area was carried out 39 samplings, in which we recorded 34 species (seven amphibians and 27 reptiles; Table 1). The amphibian species belong to four families (Craugastoridae, Eleutherodactylidae, Hylidae, and Ranidae) and four genera. Among reptiles we recorded two turtle species (*Rhinoclemmys pulcherrima* and *Kinosternon integrum*), 11 lizards, and 14 snake species, with the families Colubridae and Dipsadidae the most diverse in species, with 10 and 15, respectively (Table 1).

Species accumulation curves, completeness of the inventory and abundance of amphibians and reptiles inside of REBSSJ

In this area we recorded a total of seven amphibian species. The ACE and Chao 1 estimators predicted seven species each (Figure 2a); therefore, we obtained a completeness of 100%. On the other hand, we recorded in this reserve 27 species of reptiles, and both estimators predicted 44 and 36 species, respectively (Figure 2b), with a completeness of 60.7 and 72.9%. According to estimators, it is expected to record between nine and 17 species for achieving to the asymptote and completeness of the inventory (Figure 2b).

Table 1. List of species of amphibians and reptiles of Sierra San Juan, Nayarit, and Biosphere Reserve Sierra San Juan (RBSSJ) (X = occurrence). The code of each species used in the curves of rank-abundance (Code) is provided. Also, E = endemic to Mexico, protection category according to the Mexican Official Standard NOM-059 (Pr = Special protection, A = endangered), and International Union for Conservation of Nature (IUCN, Lc = Leas Concern, Dd = Deficient data, V = Vulnerable, NT = Near Threatened, NC = Not Consider), are provided. The population status (STAT POP; S = Stable, I = Increasing, U = Unknown, D = Decreasing, NC = Not Consider) and the value of environmental vulnerability index according to Wilson et al. (2013a, b) (EVS for its acronym in English; L = low [3-9], M = medium [10-13], H = high [14-20]; ?= not tested) are shown.

Species	Code	Endemism	NOM-059	IUCN	STAT POP	EVS	Inside RBSSJ	Outside RBSSJ
Class Amphibia								
Order Anura								
Family Bufonidae								
Incilius mazatlanensis	1	E		Lc	S	12 (M)		X
Rhinella marina	2			Lc	I	3 (L)		X
Family Craugastoridae								
Craugastor augusti	3			Lc	S	8 (L)	X	
C. occidentalis	4	E		DD	U	13 (M)	X	X
C. pygmaeus	5			Vu	D	9 (L)	X	X
C. vocalis	6	E		Lc	D	13 (M)		X
Family Eleutherodactylidae								
Eleutherodactylus nitidus	7	E		Lc	S	12 (M)	X	X
E. pallidus	8	E	Pr	DD	U	17 (H)	X	X
Family Hylidae								
Agalychnis dacnicolor	9	E		Lc	S	13 (M)		X
Exerodonta smaragdina	10	E	Pr	Lc	S	12 (M)		X
Sarcohyla bistincta	11	E	Pr	Lc	D	9 (L)	X	X
Smilisca baudinii	12			Lc	S	3 (L)		X
Tlalocohyla smithii	13	E		Lc	D	11 (M)		X
Family Ranidae								
Lithobates magnaocularis	14	E		Lc	U	12 (M)	X	X
L. pustulosus	15	E	Pr	Lc	S	9 (L)		X
Class Reptilia								
Order Testudines								
Family Geoemydidae								
Rhinoclemmys pulcherrima	16		A	NC	NC	8 (L)	X	X
Family Kinosternidae								
Kinosternon integrum	17	E	Pr	Lc	S	11 (M)	X	X
Order Squamata								
Family Anguidae								
Elgaria kingii	18		Pr	Lc	S	10 (M)	X	X
Family Dactyloidae								
Anolis nebulosus	19	E		Lc	S	13 (M)	X	X
Family Gekkonidae								
Hemidactylus frenatus	20			Lc	S		X	X
Family Helodermatidae								
Heloderma horridum	21		A	Lc	D	11 (M)	X	

Species	Code	Endemism	NOM-059	IUCN	STAT POP	EVS	Inside RBSSJ	Outside RBSSJ
Family Iguanidae								
Ctenosaura pectinata	22	E	A	NC	NC	15 (H)		X
Family Phrynosomatidae								
Sceloporus asper	23	E	Pr	Lc	D	14 (H)	X	X
S. horridus	24	E		Lc	S	11 (M)		X
S. melanorhinus	25			Lc	S	9 (L)		X
S. torquatus	26			Lc	S	11 (M)	X	
S. unicanthalis	27	E		NC	NC	?	X	
S. utiformis	28	E		Lc	S	15 (H)	X	X
Family Scincidae								
Plestiodon sp	29	E		NC	NC	?	X	X
Family Teiidae								
Aspidoscelis costata	30	E	Pr	NC	NC	11 (M)	X	X
Holcosus sinister	31			NC	NC	?	X	X
Family Boidae								
Boa sigma	32	E	A	NC	NC	10 (M)	X	X
Family Colubridae								
Coluber mentovarius	33			Lc	U	6 (L)		X
Drymarchon melanurus	34			Lc	S	6 (L)	X	X
Drymobius margaritiferus	35			NC	NC	6 (L)		X
Lampropeltis triangulum	36		A	NC	NC	7 (L)	X	X
Leptophis diplotropis	37	E	A	Lc	S	14 (H)		X
Mastigodryas melanolomus	38			Lc	S	6 (L)	X	X
Oxybelis aeneus	39			NC	NC	5 (L)		X
Senticolis triaspis	40			Lc	S	6 (L)		X
Tantilla calamarina	41	E	Pr	Lc	S	12 (M)		X
Trimorphodon tau	42			Lc	S	13 (M)	X	X
Family Dipsadidae								
Geophis dugesii	43			Lc	U	13 (M)	X	
Leptodeira splendida	44	E		Lc	U	14 (H)		X
Rhadinaea hesperia	45	E	Pr	Lc	S	10 (M)	X	X
R. taeniata	46	E		Lc	S	13 (M)	X	X
Sibon nebulatus	47			NC	NC	5 (L)		X
Family Elapidae								
Micrurus distans	48	E	Pr	Lc	S	14 (H)	X	
M. proximans	49	E	Pr	Lc	U	18 (H)	X	X
Family Leptotyphlopidae								
Rena humilis	50			Lc	S	8 (L)	X	X
Family Natricidae								
Storeria storerioides	51	E		Lc	S	11 (M)	X	
Family Typhlopidae								
Indotyphlops braminus	52			NC	NC	?		X
Family Viperidae								
Agkistrodon bilineatus	53		Pr	NT	D	11 (M)		X
Crotalus basiliscus	54	E	Pr	Lc	S	16 (H)	X	X
C. campbelli	55	E		NC	NC	?	X	

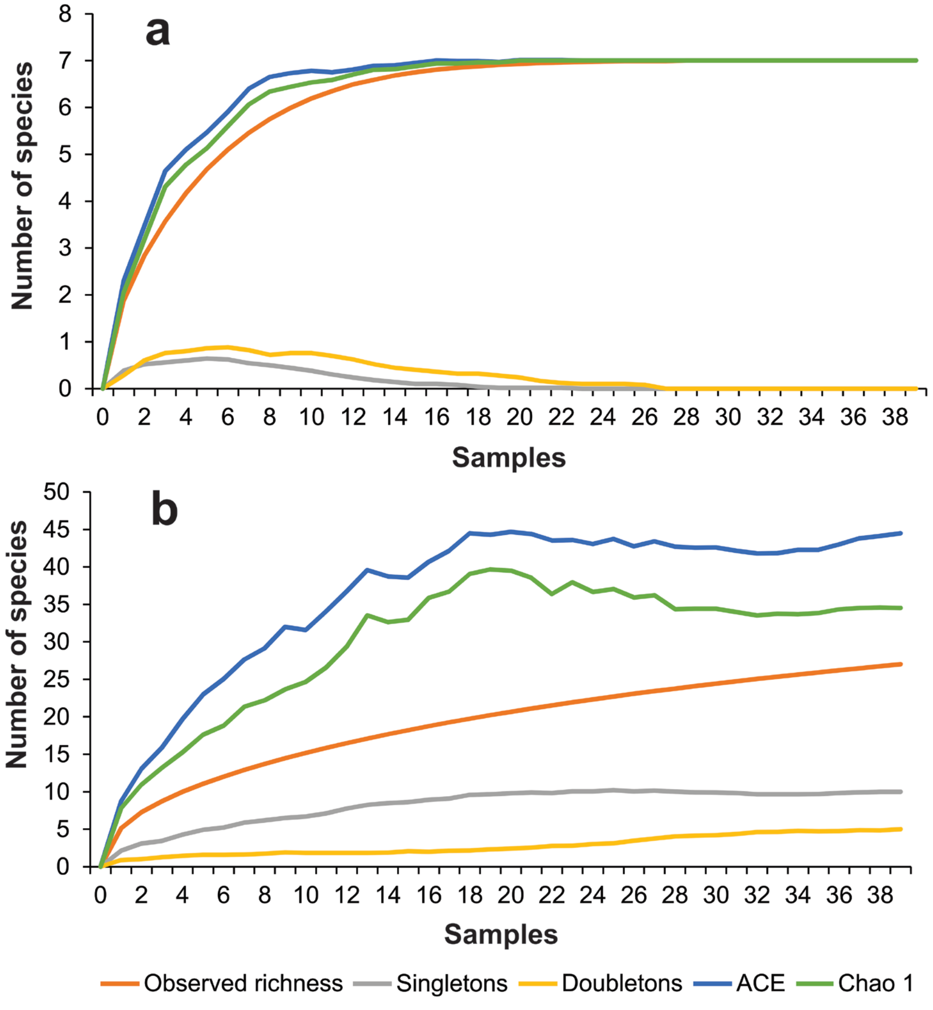

Figure 2. Species-accumulation curve for amphibians (**a**) and reptiles (**b**) inside of REBSSJ. Observed richness, species represented by a single individual (singletons), species with two individuals (doubletons), and estimated species (ACE and Chao 1).

According to abundance, for amphibians, rank–abundance curves indicated that the dominant species inside of the reserve was *Craugastor occidentalis*, and the species with less dominance was *C. augusti* (Figure 3a). Among reptiles, the analysis was divided into lizards and snakes. Rank–abundance curves showed that *Anolis nebulosus* was the most abundant species, and the least abundant were *Sceloporus utiformis* and *S. asper* (Figure 3b). Three species, *Hemidactylus frenatus*, *Heloderma horridum*, and *S. unicanthalis* were represented by one individual (Figure 3b). Among snakes, *Rhadinaea taeniata* was the most abundant species, while *Boa sigma*, *Rena humilis*, *Storeria storerioides*, *Trimorphodon tau*, and *Micrurus proximans* were represented by only one specimen each (Figure 3c).

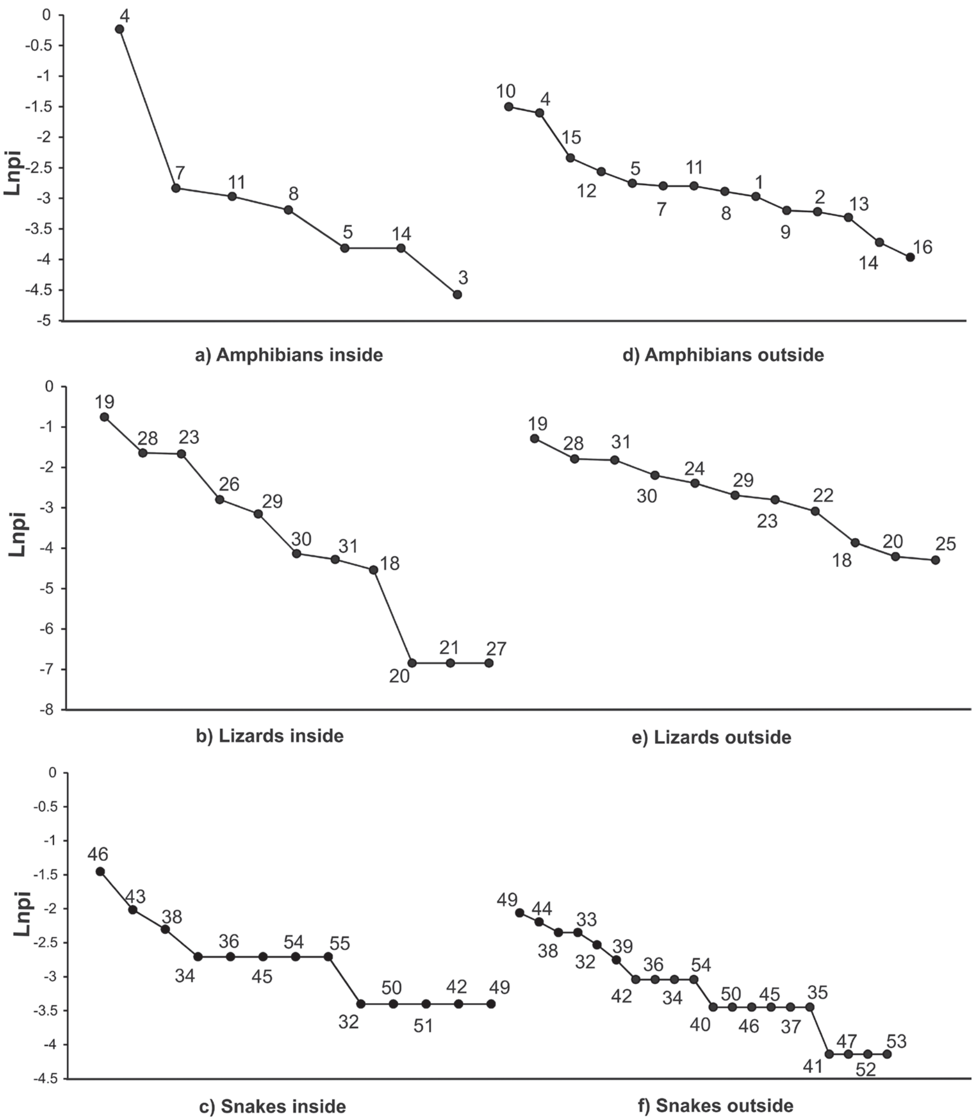

Figure 3. Rank-abundance curves for species of amphibians, lizards, and snakes inside (**a, b, c**), and outside (**d, e, f**) of the REBSSJ. Numbers refers to the acronyms of the species listed in Table 1.

Herpetofauna outside of REBSSJ

In this area we carried out 39 samplings. The species list for this area consists of 47 species (14 amphibians and 33 reptiles; Table 1). Amphibian species are represented by five families, with Hylidae the most diverse with five species (Table 1). Among reptiles, two turtle species are included in one family each (Table 1). Of 11 lizard species, four are included in the family Phrynosomatidae, and of the 20 snake species, 12 are included in Colubridae, which is the most diverse (Table 1).

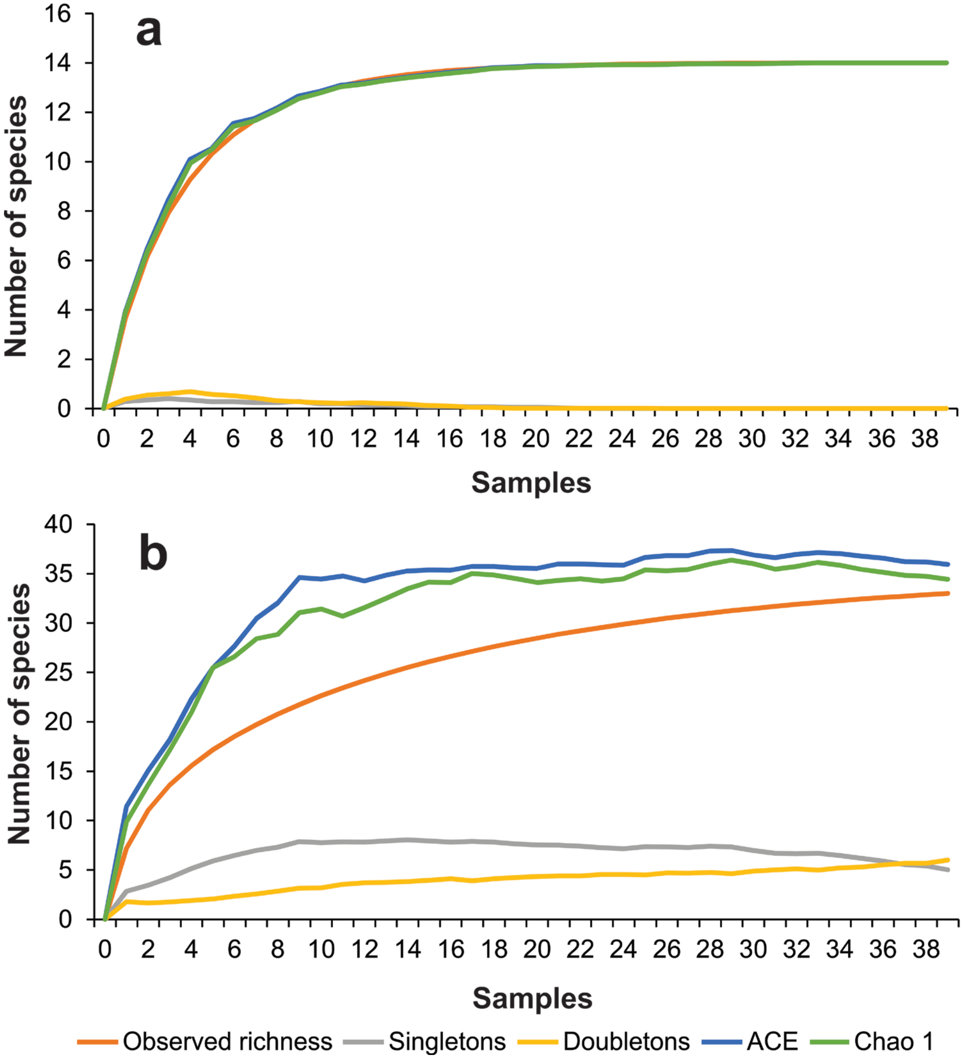

Figure 4. Species-accumulation curve of amphibians (**a**) and reptiles (**b**) outside REBSSJ. Observed richness, species represented by a single individual (singletons), species with two individuals (doubletons), and estimated species (ACE and Chao 1).

Species accumulation curves, completeness of the inventory and abundance of amphibians and reptiles outside of REBSSJ

Outside of REBSSJ was recorded a total of 14 amphibian species. Non-parametric estimators ACE and Chao 1 predicted 14 species each (Figure 4a), which showed a completeness of 100%. Among reptiles, we recorded a total of 33 species, and the estimators ACE and Chao 1 predicted 35.9 and 34.4 species, respectively (Figure 4b), obtaining a completeness of 91.8 and 95.8%, respectively (Figure 4b).

Respect to abundance, in amphibians, *Exerodonta smaragdina* was the most abundant species, followed by *C. occidentalis* (Figure 3d), and the least abundant was *C. vocalis* (Figure 3d). Among reptiles, lizard species were the most abundant in this environment, with the dominant species being *A. nebulosus*, *S. utiformis*, and *Holcosus sinister*. On the other hand, *Elgaria kingii*, *H. frenatus*, and *S. melanorhinus* presented a low individual number each (Figure 3e). Among snakes, the most abundant species were *M. proximans*, *Leptodeira splendida*, and *Mastigodryas melanolomus*; in contrast, *Tantilla calamarina*, *Sibon nebulatus*, *Indotyphlops braminus*, and *Agkistrodon bilineatus* were represented by one specimen each (Figure 3f).

Beta diversity

According to the values of completeness, we observed similar values of species composition of amphibians and reptiles in both inside and outside environments. Among amphibians, the completeness value between sites was 0.60, and among reptiles 0.50, which indicates an intermediate complementarity in species composition among these environments.

Comparison inside vs. outside of the reserve

In general, a high pattern in species richness, diversity, and abundance of amphibians and reptiles was found outside rather than inside the reserve (Table 2; Figures 5 and 6a–c). The analysis of true diversity showed remarkable differences between environments; outside the reserve showed the highest values for both amphibian and reptiles (Table 2). According to species richness and abundance, outside of the reserve was found to have double of the number of amphibian species and number of individuals by species than inside the reserve (Figure 6a). This pattern was similar in snakes, where outside of the reserve we found 20 species distributed among 64 individuals, whereas inside were 14 species scattered among 30 individuals (Figure 6c). Both inside and outside of the reserve we found the same species of turtles, but outside the density was higher than inside (Table 2). Inside of the reserve, however, lizard density was higher (103 individuals) than outside, with both environments containing 11 species (Figure 6b; Table 2).

Functional guilds inside vs outside of the reserve

Functional richness, functional equality, and functional dispersion indices were higher for amphibians outside the reserve (Table 3). For reptiles, functional richness and functional dispersion indices were found to be higher outside the reserve (Table 3). The greatest contributions of richness and functional dispersion are given by the features and niches exploited by species of the genera *Sceloporus*, *Ctenosaura*, and *Hemidactylus.* Functional equity was found to be almost equal in both sites.

Table 2. Summary of values of diversity and abundance by taxonomic group registered inside and outside REBSSJ, Nayarit, Mexico.

Group	Total species	Species richness		Abundance		True diversity		Shared species
		inside	outside	inside	outside	inside	outside	
Amphibians	15	7	14	680	1199	2.33	9.6	6
Tortoises	2	2	2	4	8			
Lizards	14	11	11	937	834	4.42	7.96	8
Snakes	24	14	20	30	64	2.35	16.47	10
Totals	55	34	47	1651	2105			

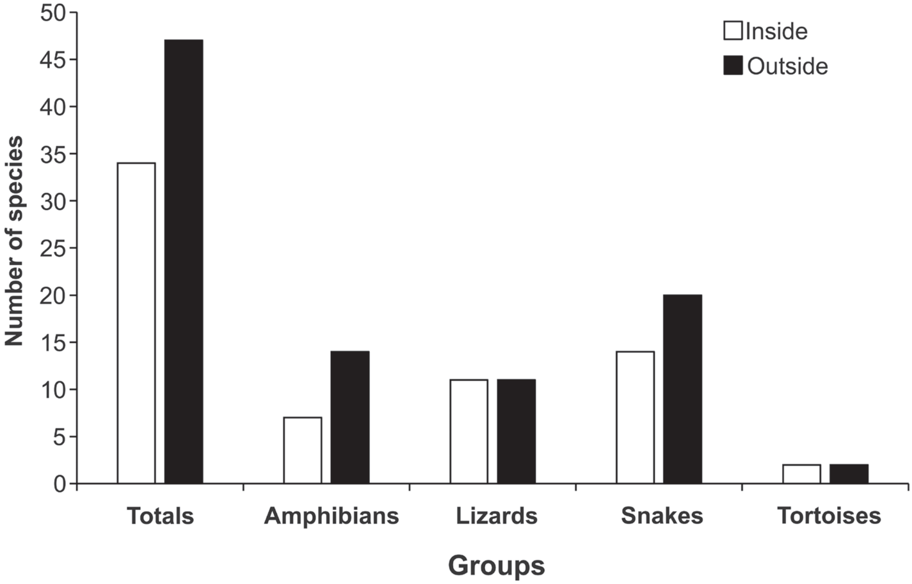

Figure 5. Graphic comparison of the number of species (total and by taxonomic group) inside and outside of REBSSJ.

Table 3. Functional richness (Fr), functional equity (Fe), and functional dispersion (Fd) of herpetofauna inside and outside of REBSSJ, Nayarit, Mexico.

	Amphibians			Reptiles		
	Fr	Fe	Fd	Fr	Fe	Fd
Inside	2.55	0.28	1.39	8.13	0.37	1.93
Outside	3.98	0.37	2.64	8.91	0.38	2.83

Protected species inside vs outside of the reserve

Outside the reserve we recorded a higher species number under some category of risk in national regulation according the NOM-059 (DOF 2010), also by the international list of the IUCN, and by using Environmental Vulnerability Score (EVS) algorithm (Table 4).

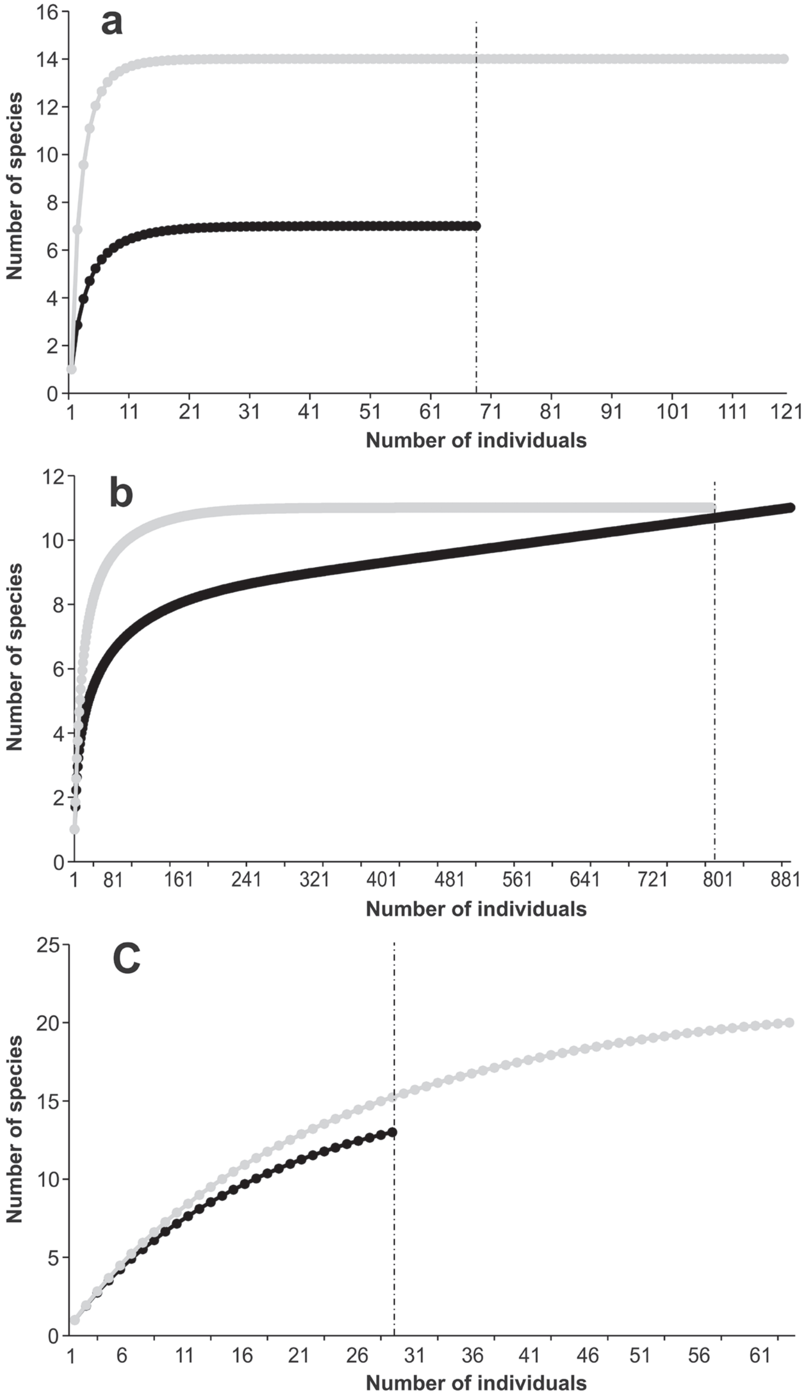

Figure 6. Rarefaction curves of species of amphibians (**a**), lizards (**b**), and snakes (**c**). Richness is compared inside black line and outside gray line of REBSSJ. Vertical line refers to the minimum number of individuals between sites.

Table 4. Number of species under different risk categories indicated by the national and international regulations (NOM-059, IUCN 2016), and environmental vulnerability index (EVS).

Normative	Category	Amphibians		Reptiles	
		inside	outside	inside	outside
IUCN	Least concern	4	11	19	21
	Vulnerable	1	1		
	Near Threatened				1
	Deficient Data	2	2		
	Not Consider			8	11
Population status (IUCN)	Decreasing	2	4	2	2
	Stable	2	6	15	17
	Increasing		1		
	Unknown	3	3	2	3
	Deficient data			8	11
Endemisms	Endemic	5	11	15	16
	No endemic				
NOM-059	Pr	2	4	8	9
	A			4	5
EVS	Low	3	5	5	11
	Medium	3	8	12	11
	High	1	1	5	7
	No evaluated			4	3

Discussion

The herpetofauna of Nayarit had been ignored for a long time (Flores-Villela et al. 2004). Currently, however, it is known that the state has 154 species, including 34 anurans, two salamanders, one crocodylian, 107 squamates, and 10 turtles (Woolrich-Piña et al. 2016). In this study we recorded for the entire Sierra San Juan a total of 55 species, representing 35.5% of the state herpetofauna. Of this number of species, the area corresponding to REBSSJ has a herpetofauna of 34 species. Woolrich-Piña et al. (2016) mentioned that the herpetofauna of REBSSJ is composed by 73 species of amphibians and reptiles (19 anurans, 52 squamates, and two turtles). This number of species, however, was taken from the literature; only occasionally one of the authors visited the REBSSJ. Our results are the product of 39 months of fieldwork, which shows that the herpetofauna inside REBSSJ is composed of seven species of anurans, 25 squamates, and two tortoises. Our accumulation curves shows that our inventory of amphibians is complete and for reptiles between nine and 17 species are expected to be recorded in order to achieve the asymptote and completeness of the inventory. Thus, Woolrich-Piña et al. (2016) results overestimated the herpetological biodiversity inside the reserve because they did not conduct a systematic field sampling. In this sense, monitoring and field studies in natural protected area, as well as its surrounding areas represent the best strategies for documenting species richness, as well as diverse aspects of the recorded species, such as natural history, population density, and communities structure (Ervin 2003, Rodrigues et al. 2004). In addition to the bibliographic review and revision of data bases are important sources for evaluating and the decree of the natural protected areas (Ervin 2003).

Inside of REBSSJ was found a lower species number than outside of this NPA. This pattern is similar to that seen in other studies that analyzed species richness and abundance of species from different biological groups inside and outside of a NPA as mammals (Decher and Bahian 1999, Caro 2001), birds (Herremans 1998), and fungi (Bhagwat et al. 2005). In this study we recorded a remarkable increase in species richness and abundance of the herpetofauna outside the reserve. This difference could be explained by environmental heterogeneity among areas, which generates edge effect (Schlaepfer and Gavin 2001), and modification of the environment toward agroecosystems, such as shade coffee plantations (Pineda et al. 2005), and land-use change involving grazing areas (Gardner et al. 2007). For example, in two different studies by Bell and Donnelly (2006) and Berriozabal-Islas et al. (2017), with amphibians and reptiles in the former, and with lizard in the last; in both studies the composition of communities was different to those preserved environments. These studies found a decrease in species richness and diversity to transformed environments. These results show a remarkable difference in species richness and composition of communities among areas (Gardner et al. 2007, Berriozabal-Islas et al. 2017).

Inside the REBSSJ we recorded a lower species number of amphibian and reptiles, with *Craugastor* of the former group the dominant genus. Species of this genus are associated with temperate environments, such as pine forest and pine-oak forest, which were dominant in this area of the reserve (Meza-Parral and Pineda 2015). This pattern is promoted by the vegetation cover of the area, as shown in other studies (Urbina-Cardona et al. 2006, Cruz-Elizalde et al. 2016). Although inside the reserve there exists a higher portion of preserved forest, without apparent agricultural modification, in this area only a species of hylid frog (*Sarcohyla bistincta*) occurs; in contrast, outside of the reserve we recorded five species of hylid frogs (*Agalychnis dacnicolor*, *E. smaragdina*, *S. bistincta*, *Smilisca baudinii*, and *Tlalocohyla smithii*). These results, in the former case, might be associated with the fact that inside the reserve there are no permanents water bodies, which provide the necessary requirements for these kind of species (Wiens et al. 2006), although inside of the reserve there is a high proportion of tree coverage, mainly oak-pine forest and cloud forest (Téllez 1995) in which these species are distributed (Wiens et al. 2006, Cruz-Elizalde et al. 2016). In the latter case, the result might be due to the fact that outside the reserve there exist patches of tropical vegetation, such as semi-deciduous rainforest and cloud forest with temporary streams that provide the necessary requirements for species reproduction, and therefore, a high species diversity of this group (Pineda et al. 2005, Wiens et al. 2006). This pattern is similar to those reported for tropical environments from low elevations, where the species diversity of the family Hylidae was high (Pineda et al. 2005, Cruz-Elizalde et al. 2016).

It is well known that the NPAs are important for nature conservation (Ervin 2003). This study showed that places outside the reserve are represented by cultivated zones of mango and avocado, grazing areas, and shade coffee plantations, which maintain a high species richness and abundance for both amphibians and reptiles. In this sense it has been reported that the surrounding matrix of the protected areas plays an important role in the protection of some species (Halpin 1997, Hannah et al. 2002), in particular for those species with high mobility (Estrada et al. 1994, Caro 2001). Halpin (1997) and Hannah et al. (2002) coincide that climate change affect the structure and dynamics of the landscape, mainly in natural protected areas. These authors pointed out that due to climatic change, diverse species can change their range of migration at large scale (Peters and Darling 1985), and at local scale, their altitudinal distribution in a linear way, mainly in mountains (Peters and Darling 1985, Halpin 1997, Hannah et al. 2002), modify species composition inside and outside of reserves or preserved environments (Halpin 1997). These patterns of variation of species among areas have been tested in mammals of rain forest in Los Tuxtlas, Mexico (Estrada et al. 1994), or inside and outside of natural protected area from Tanzania (Caro 2001). Among reptiles, lizards and snakes showed two patterns in richness and abundance between sites. Lizards, both inside and outside the reserve showed similar species number (11 species); however, inside of the reserve a high number of individuals occurred than outside. In this sense, species that occurred in both inside and outside of the reserve were of the genus *Sceloporus*, which showed tolerance for the transformed environments due to physiological advantages as impermeable skin or high tolerance to aridity, use a high diversity of environments, and diversity of habits (e.g., saxicolous, arboreal; Macip-Ríos and Muñoz-Alonso 2008). These patterns have been promoted by heterogeneous environments that are reflected in a high number of microhabitats, such as logs, rocks, holes, accumulated rocks, left litter, open areas, which in turn will generate perch sites (Luja et al. 2008). These conditions are favorable to *S. utiformis* and *A. nebulosus* because they were dominant species in both inside and outside the reserve. This dominant pattern has been reported in lizard species from tropical environments (Gardner et al. 2007, Vitt et al. 2007).

Among snakes, a high number of species and individuals were found outside of the reserve. This phenomenon is explained by the high dispersal capacity of this group of reptiles, species of which have a larger home range than do lizard species (Vitt et al. 2007). In addition, most of the recorded snakes are nocturnal; therefore, the occurrence outside of the reserve might be related to the presence of water bodies, where abundance of the amphibians is high, with these snakes feeding on this group (Cadle and Greene 1993, França et al. 2008).

Studies on fragmented tropical environments show that the transformation of environments reduces the alpha diversity, but increase the diversity at a landscape level (Vitt and Caldwell 2001). This pattern is similar to our results, because species composition for both communities (inside and outside) was complementary. For example, inside the reserve, the amphibian *C. augusti* was the exclusive species, and *Incilius mazatlanensis* and *Rhinella marina* were exclusive outside of the reserve. Similar patterns occurred in lizards and snakes; places outside the reserve had a higher number of exclusive species, such as *Drymobius margaritiferus*, *Oxybelis aeneus*, and *A. bilineatus* inhabiting tropical environments (França et al. 2008).

In addition to remarkable differences in species richness and abundance of amphibian and reptiles between sites, outside the reserve we recorded higher scores of functional diversity in both amphibians and reptiles. Such differences suggest a more complex network of interactions among the components of biodiversity outside the reserve. Outside the reserve there is a more heterogeneous landscape, which gives the species the opportunity to diversify in terms of guilds (habitat, food, or habits). Therefore, if these sites are not considered within the measures of conservation, biodiversity will be severely eroded. Finally, outside the reserve we found a major species number under some category of protection of the IUCN (2016), NOM-059, as well a high species number under the category of medium environmental vulnerability (Table 4). This reserve belongs to an important region in the context of biodiversity, because currently new forms of amphibian species have been recognized there (Caviedes-Solís et al. in preparation), which suggests that species richness for this area will increase in the future.

Our results suggest that in addition to protecting the area designated as NPA's, studies in surrounding areas should be carried out to consider the possibility of protecting a greater amount of habitat that should include semi-deciduous tropical forest and cloud forest to conserve a higher number of species (Toledo and Fernades Batista 2012). In this sense, the analyzed areas require a good programs of plans and management for conservation of the reserve and its boundaries (Herremans 1998, Caro 2001, Bhagwat et al. 2005, Becker et al. 2010).

Implications for conservation of herpetofauna in natural protected areas in tropical environments

Land use change is the main cause of the loss of diversity in the last decades (Ervin 2003, Hayes 2006), being tropical regions strongly threatened (Laurence et al. 2012). The decree of NPA´s in tropical environments is the main measures to conservation of diversity (Bruner et al. 2001, Rodrigues et al. 2004); however, effectiveness of the reserve for conservation depends of diverse factors, such as environmental heterogeneous, size of patch, and connectivity with other reserves, as land use inside and outside of the natural protected area (Juárez-Ramírez et al. 2016).

Bruner et al. (2001) evaluated the effectiveness of the natural protected areas in tropical countries with high anthropogenic threats, and recorded that most of the cases, natural protected areas fulfill conservation function, in addition to mitigation the anthropic effect. In this sense, for amphibians and reptiles is essential evaluation of the effectiveness of the NPA´s on their populations conservation and the impact of its surrounding areas (Suazo-Ortuño et al. 2015). To date there is a sufficient number of studies analyzing fragmentation effect on tropical environments (Pineda et al. 2005, Gardner et al. 2007, Macip-Ríos and Muñoz-Alonso 2008, Cruz-Elizalde et al. 2016), however, there are few studies analyzing the NPA´s, as well as the effect of surrounding matrix (Laurence et al. 2012).

Herpetofauna inside of the NPA´s have been analyzed in several studies from tropical environments of the world (Bruner et al. 2001, Bell and Donelly 2006, Gardner et al. 2007, Laurence et al. 2012), but very few in tropical environments from Mexico (Vite-Silva et al. 2010, Suazo-Ortuño et al. 2015, Berriozabal-Islas et al. 2017). These studies show a general pattern of species loss of the NPA´s toward surrounding and fragmented environments (Suazo-Ortuño et al. 2015). When comparing these results with our data, it showed a different pattern, with a higher species richness, diversity and abundancy of amphibians and reptiles outside of the NPA than inside. Species richness and diversity recorded inside and outside of the NPA´s may differ among biological groups, being more significant in vertebrate group with low vagility, such as amphibians and reptiles (Pineda et al. 2005, Berriozabal-Islas et al. 2017) than those with high movements, as mammals (Caro 2001), or birds (Herremans 1998). This response is influencing by degradation and modification of the landscape around of an NPA (Laurence et al. 2012), due to areas under protection are isolated and is generated an edge effect, and therefore, modifications in environmental parameters (e. g., temperature, solar radiation) and ecological (e. g., habitat and microhabitats availability) that affect population density (Pineda et al. 2005). Therefore, landscape modification also promotes a high number of habitats and conditions that favors a higher number of generalist species (Caro 2001, Cruz-Elizalde et al. 2016) than those occupying particular microhabitats or are in restricted to a single environmental type (Wiens et al. 2006).

Considering to the results showed in this study, where outside of the NPA is reported a higher number of species, higher functional diversity, and higher species number under high categories of conservation, we suggest the following measures to be considered in future studies that compare the herpetofauna inside and outside of an NPA´s: i) to analyze the status of conservation under different national (e. g., NOM-059), and international regulations (e.g., IUCN) of the species (Wilson et al. 2013a, b, Cruz-Elizalde et al. 2016); ii) to evaluate ecotones among areas that comprise the NPA´s and surrounding environments (Pineda et al. 2005); iii) to analyze species richness and diversity considering environmental factors, such as vegetal cover, temperature, solar radiation, and resources availability among different environments (Urbina-Cardona et al. 2006, Vitt et al. 2007), and iv) to evaluate the partition of the diversity at regional level and consider the functional and phylogenetic diversity of the communities inside and outside of the NPA´s (Cruz-Elizalde et al. 2016, Berriozabal-Islas et al. 2017).

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References

Becker CG, Loyola RD, Haddad CF, Zamudio K (2010) Integrating species life-history traits and patterns of deforestation in amphibian conservation planning. Diversity and Distributions 16: 10–19. https://dx.doi.org/10.1111/j.1472-4642.2009.00625.x

Bell KE, Donnelly MA (2006) Influence of forest fragmentation on community structure of frogs and lizards in Northeastern Costa Rica. Conservation Biology 20: 1750–1760. https://dx.doi.org/10.1111/j.1523-1739.2006.00522.x

Berriozabal-Islas C, Badillo-Saldaña LM, Ramírez-Bautista A, Moreno CE (2017) Effects of habitat disturbance on lizard functional diversity in a tropical dry forest of the Pacific Coast of Mexico. Tropical Conservation Science 10: 1–11. https://doi.org/10.1177/1940082917704972

Bhagwat S, Kushalappa C, Williams P, Brown N (2005) The role of informal protected areas in maintaining biodiversity in the Western Ghats of India. Ecology and Society 10: 8. http://www.ecologyandsociety.org/vol10/iss1/art8/

Blackman A, Pfaff A, Robalino J (2015) Paper park performance: Mexico's natural protected areas in the 1990s. Global Environmental Change 31: 50–61. http://dx.doi.org/10.1016/j.gloenvcha.2014.12.004

Bojórquez I (2003) Estudio técnico justificativo de la sierra de San Juan, Nayarit, para su declaratoria como área natural protegida. INADES-UAN.

Bruner AG, Gullison RE, Rice RE, da Fonseca GAB (2001) Effectiveness of Parks in Protecting Tropical Biodiversity. Science 291: 125–128. http://dx.doi.org/10.1126/science.291.5501.125

Cadle JE, Greene HW (1993) Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. In: Ricklefs RE, Schluter D (Eds) Species diversity in ecological communities: Historical and geographical perspectives. University of Chicago Press, Chicago, 281–293.

Canseco-Márquez L (2007) *Geagras redimitus*. The IUCN Red List of Threatened Species 2007: e.T63786A12708878. http://dx.doi.org/10.2305/IUCN.UK.2007.RLTS.T63786A12708878 [Accessed 14 April 2016]

Caro TM (2001) Species richness and abundance of small mammals inside and outside an African national park. Biological Conservation 98: 251–257. http://dx.doi.org/10.1016/S0006-3207(00)00105-1

Casas-Andreu G, Valenzuela-López G, Ramírez-Bautista A (1991) Cómo hacer una colección de anfibios y reptiles. Cuadernos del Instituto de Biología, UNAM, México, D.F., 1–68.

Casanoves F, Pla L, Di Rienzo JA, Díaz S (2011) FDiversity: a software package for the integrated analysis of functional diversity. Methods in Ecology and Evolution 2: 233–237. http://dx.doi.org/10.1111/j.2041-210X.2010.00082.x

Chape S, Harrison J, Spalding M, Lysenko I (2005) Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Philosophical Transactions of the Royal Society of London B: Biological Sciences 360: 443–455. http://dx.doi.org/10.1098/rstb.2004.1592

Colwell RK (2005) EstimateS: ver. 7.5. Statistical estimation of species richness and shared species from samples.

Colwell R, Coddington J (1994) Estimating terrestrial biodiversity through exploration. Philosophical Transactions of the Royal Society of London B: Biological Sciences 345: 101–118. http://dx.doi.org/10.1098/rstb.1994.0091

CONANP (2017) Comisión Nacional de Áreas Naturales Protegidas, ¿Qué hacemos? http://www.conanp.gob.mx/que_hacemos [Accessed: 9 July 2017]

Cruz-Elizalde R, Berriozabal-Islas C, Hernández-Salinas U, Martínez-Morales MA, Ramírez-Bautista A (2016) Amphibian species richness and diversity in a modified tropical environment of central Mexico. Tropical Ecology 57: 407–417.

Decher J, Bahian LK (1999) Diversity and structure of terrestrial small mammal communities in different vegetation types in the Accra Plains of Ghana. Journal of Zoology 247: 395–408. http://dx.doi.org/10.1111/j.1469-7998.1999.tb01002.x

DOF (Diario Oficial) (2010) Norma Oficial Mexicana NOM-059-SEMARNAT-2010. Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-lista de especies en riesgo, 77 pp.

Espinosa IJA (2000) Distribución de la riqueza, endemismo y rareza: criterios para la conservación de las aves de la Sierra de San Juan, Nayarit, México. Dissertation Universidad Nacional Autónoma de México.

Estrada A, Coates-Estrada R, Merritt Jr D (1994) Non-flying mammals and landscape changes in the tropical rain forest of Los Tuxtlas, Mexico. Ecography 17: 229–241. http://dx.doi.org/10.1111/j.1600-0587.1994.tb00098.x

Ervin J (2003) Protected area assessments in perspective. BioScience 53: 819–822. https://dx.doi.org/10.1641/0006-3568(2003)053[0819:PAAIP]2.0.CO;2

Feinsinger P (2003) El diseño de estudios de campo para la conservación de la biodiversidad. FAN (Fundación Amigos de la Naturaleza), Santa Cruz de la Sierra, Bolivia, 242 p.

Figueroa F, Sánchez-Cordero V (2008) Effectiveness of natural protected areas to prevent land use and land cover change in Mexico. Biodiversity and Conservation 17: 3223–3240. http://dx.doi.org/10.1007/s10531-008-9423-3

Flores-Villela OA, Smith HM, Chiszar D (2004) The history of herpetological exploration in Mexico. Bonner Zoologische Beiträge 52: 311–35.

França FGR, Mesquita DO, Nogueira CC, Araújo AFB (2008) Phylogeny and ecology determine morphological structure in a snake assemblage in the Central Brazilian Cerrado. Copeia 1: 23–38. http://dx.doi.org/10.1643/CH-05-034

García E (1988) Modificaciones al sistema de clasificación climática de Köppen (para adaptarlo a las condiciones de la República Mexicana). Instituto de Geografía, UNAM. México, DF.

Gardner TA, Ribeiro-Júnior MA, Barlow J, Ávila-Pires TCS, Hoogmoed MS, Peres CA (2007) The value of primary, secondary, and plantation forests for a Neotropical herpetofauna. Conservation Biology 21: 775–787. http://dx.doi.org/10.1111/j.1523-1739.2007.00659.x

González RE (2010) La Reserva Ecológica Sierra de San Juan a 23 años del decreto. Revista Fuente 4: 5–9.

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379–391. http://dx.doi.org/10.1046/j.1461-0248.2001.00230.x

Halpin PN (1997) Global climate change and natural-area protection: management responses and research directions. Ecological Applications 7: 828–843. http://dx.doi.org/10.1890/1051-0761(1997)007[0828:GCCANA]2.0.CO;2

Hannah L, Midgley GF, Millar D (2002) Climate change-integrated conservation strategies. Global Ecology and Biogeography 11: 485–495. http://dx.doi.org/10.1046/j.1466-822X.2002.00306.x

Hammer Ø, Harper DAT, Ryan PD (2001) Past: Paleontological statics software package for evaluation and data analysis. Paleontologica Electronica 4: 9.

Hayes TM (2006) Parks, people, and forest protection: an institutional assessment of the effectiveness of protected areas. World Development 34: 2064–2075. http://dx.doi.org/10.1016/j.worlddev.2006.03.002

Herremans M (1998) Conservation status of birds in Botswana in relation to land use. Biological Conservation 86: 139–160. http://dx.doi.org/10.1016/S0006-3207(98)00016-0

Jiménez-Valverde A, Hortal J (2003) Las curvas de acumulación de especies y la necesidad de evaluar los inventarios biológicos. Revista Ibérica de Aracnología 8: 151–161.

Juárez-Ramírez MC, Aguilar-López JL, Pineda E (2016) Protected natural areas and the conservation of amphibians in a highly transformed mountainous region in Mexico. Herpetological Conservation and Biology 11: 19–28.

IUCN (2016) The IUCN Red List of Threatened Species. Version 2015.4. http://www.iucnredlist.org [Accessed 12 April 2016]

Jost L (2006) Entropy and diversity. Oikos 113: 363–375. http://dx.doi.org/10.1111/j.2006.0030-1299.14714.x

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91: 299–305. http://dx.doi.org/10.1890/08-2244.1

Laurence WF, Useche DC, Rendeiro J, Kalka M, Bradshaw CJA, Sloan SP, Laurance SG, Campbell M, Abernethy K, Alvarez P, Arroyo-Rodriguez V, Ashton P, Benítez-Malvido J, Blom A, Bobo KS, Cannon CH, Cao M, Carroll R, Chapman C, Coates R, Cords M, Danielsen F, De Dijn B, Dinerstein E, Donnelly MA, Edwards D, Edwards F, Farwig N, Fashing P, Forget PM, Foster M, Gale G, Harris D, Harrison R, Hart J, Karpanty S, Kress WJ, Krishnaswamy J, Logsdon W, Lovett J, Magnusson W, Maisels F, Marshall AR, McClearn D, Mudappa D, Nielsen MR, Pearson R, Pitman N, Ploeg JVD, Plumptre A, Poulsen J, Quesada M, Rainey H, Robinson D, Roetgers C, Rovero F, Scatena F, Schulze C, Sheil D, Struhsaker T, Terborgh J, Thomas D, Timm R, Nicolas Urbina-Cardona J, Vasudevan K, Wright SJ, Arias-G JC, Arroyo L, Ashton M, Auzel P, Babaasa D, Babweteera F, Baker P, Banki O, Bass M, Bila-Isia I, Blake S, Brockelman W, Brokaw N, Brühl CA, Bunyavejchewin S, Chao JT, Chave J, Chellam R, Clark CJ, Clavijo J, Congdon R, Corlett R, Dattaraja HS, Dave C, Davies G, Beisiegel BM, de Nazaré Paes da Silva R, Di Fiore A, Diesmos A, Dirzo R, Doran-Sheehy D, Eaton M, Emmons L, Estrada A, Ewango C, Fedigan L, Feer F, Fruth B, Willis JG, Goodale U, Goodman S, Guix JC, Guthiga P, Haber W, Hamer K, Herbinger I, Hill J, Huang Z, Sun IF, Ickes K, Itoh A, Ivanauskas N, Jackes B, Janovec J, Janzen D, Jiangming M, Jin C, Jones T, Justiniano H, Kalko E, Kasangaki A, Killeen T, King HB, Klop E, Knott C, Koné I, Kudavidanage E, da Silva Ribeiro JL, Lattke J, Laval R, Lawton R, Leal M, Leighton M, Lentino M, Leonel C, Lindsell J, Ling-Ling L, Linsenmair KE, Losos E, Lugo A, Lwanga J, Mack AL, Martins M, McGraw WS, McNab R, Montag L, Thompson JM, Nabe-Nielsen J, Nakagawa M, Nepal S, Norconk M, Novotny V, O'Donnell S, Opiang M, Ouboter P, Parker K, Parthasarathy N, Pisciotta K, Prawiradilaga D, Pringle C, Rajathurai S, Reichard U, Reinartz G, Renton K, Reynolds G, Reynolds V, Riley E, Rödel MO, Rothman J, Round P, Sakai S, Sanaiotti T, Savini T, Schaab G, Seidensticker J, Siaka A, Silman MR, Smith TB, de Almeida SS, Sodhi N, Stanford C, Stewart K, Stokes E, Stoner KE, Sukumar R, Surbeck M, Tobler M, Tscharntke T, Turkalo A, Umapathy G, van Weerd M, Vega Rivera J, Venkataraman M, Venn L, Verea C, de Castilho CV, Waltert M, Wang B, Watts D, Weber W, West P, Whitacre D, Whitney K, Wilkie D, Williams S, Wright DD, Wright P, Xiankai L, Yonzon P, Zamzani F (2012) Averting biodiversity collapse in tropical forest protected areas. Nature 489: 290–294. http://dx.doi.org/10.1038/nature11318

Luhr JF (2000) The geology and petrology of Volcán San Juan (Nayarit, México) and the compositionally zoned Tepic Pumice. Journal of Volcanology and Geothermal Research 95: 109–156. http://dx.doi.org/10.1016/S0377-0273(99)00133-X

Luja VH, Herrando-Pérez S, González-Solís D, Luiselli L (2008) Secondary rain forests are not havens for reptile species in tropical Mexico. Biotropica 40: 747–757. http://dx.doi.org/10.1111/j.1744-7429.2008.00439.x

Macip-Ríos R, Muñoz-Alonso A (2008) Diversidad de lagartijas en cafetales y bosque primario en el Soconusco chiapaneco. Revista Mexicana de Biodiversidad 79: 185–195.

Magurran A (1998) Ecological biodiversity and its measurement. Princenton University Press, New Jersey.

Mason NW, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111: 112–118. http://dx.doi.org/10.1111/j.0030-1299.2005.13886.x

Meza-Parral Y, Pineda E (2015) Amphibian diversity and threatened species in a severely transformed Neotropical region in Mexico. PLoS ONE 10: e0121652. http://dx.doi.org/10.1371/journal.pone.0121652

Moreno CE (2001) Métodos para medir la biodiversidad, vol. 1. M&T-Manuales y Tesis. Sociedad Entomológica Aragonesa, Zaragoza, 84 pp.

Moreno CE, Barragán F, Pineda E, Pavón NP (2011) Reanálisis de la diversidad alfa: alternativas para interpretar y comparar información sobre comunidades ecológicas. Revista Mexicana de Biodiversidad 82: 1249–1261.

Peters RL, Darling JD (1985) The greenhouse effect and nature reserves. BioScince 35: 707–717. https://dx.doi.org/10.2307/1310052

Pineda E, Moreno C, Escobar F, Halffter G (2005) Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, México. Conservation Biology 19: 400–410. http://dx.doi.org/10.1111/j.1523-1739.2005.00531.x

Ramírez-Bautista A, Hernández-Ibarra X (2004) Ficha técnica de *Ctenosaura acanthura*. En: Arizmendi, M. C. (compilador). Sistemática e historia natural de algunos anfibios y reptiles de México. Facultad de Estudios Superiores Iztacala, Unidad de Biología, Tecnología y Prototipos (UBIPRO), Universidad Nacional Autónoma de México. Bases de datos SNIB-CONABIO. México, D.F.

Rife AN, Erisman B, Sanchez A, Aburto-Oropeza O (2013) When good intentions are not enough… Insights on networks of "paper park" marine protected areas. Conservation Letters 6: 200–212. http://dx.doi.org/10.1111/j.1755-263X.2012.00303.x

Rodrigues ASL, Andelman SJ, Bakarr MI, Boitani L, Brooks TM, Cowling RM, Fishpool LDC, da Fonseca GAB, Gaston KJ, Hoffmann M, Long JS, Marquet PA, Pilgrim JD, Pressey RL, Schipper J, Sechrest W, Stuart SN, UnderhilL LG, Waller RW, Watts MEJ, Yan X (2004)

Effectiveness of the global protected area network in representing species diversity. Nature 428: 640–643. http://dx.doi.org/10.1038/nature02422

Román-Cuesta RM, Martínez-Villalta J (2006) Effectiveness of protected areas in mitigating fire within their boundaries: case study of Chiapas, Mexico. Conservation Biology 20: 1074–1086. http://dx.doi.org/10.1111/j.1523-1739.2006.00478.x

Schlaepfer MA, Gavin TA (2001) Edge effects on lizards and frogs in tropical forest fragments. Conservation Biology 15: 1079–1090. http://dx.doi.org/10.1046/j.1523-1739.2001.0150041079.x

Suazo-Ortuño I, Alvarado-Díaz J, Mendoza E, López-Toledo L, Lara-Uribe N, Márquez-Camargo C, Paz-Gutiérrez JG, Rangel-Orozco JD (2015) High resilience of herpetofaunal communities in a human-modified tropical dry forest landscape in western Mexico. Tropical Conservation Science 8: 396–423. https://dx.doi.org/10.1177/194008291500800208

Téllez VO (1995) Flora, vegetación y fitogeografía de Nayarit, México. Dissertation, Universidad Nacional Autónoma de México.

Toledo LF, Fernandes Batista R (2012) Integrative study of Brazilian anurans: geographic distribution, size, environment, taxonomy, and conservation. Biotropica 44: 785–7912. http://dx.doi.org/10.1111/j.1744-7429.2012.00866.x

Urbina-Cardona JN, Olivares-Pérez M, Reynoso VH (2006) Herpetofauna diversity and microenvironment correlates across a pasture-edge-interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. Biological Conservation 132: 61–75. http://dx.doi.org/10.1016/j.biocon.2006.03.014

Villéger S, Mason NW, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89: 2290–2301. http://dx.doi.org/10.1890/07-1206.1

Vite-Silva VD, Ramírez-Bautista A, Hernández-Salinas U (2010) Diversidad de anfibios y reptiles de la Reserva de la Biosfera Barranca de Metztitlán, Hidalgo, México. Revista Mexicana de Biodiversidad 80: 473–485.

Vitt LJ, Caldwell JP (2001) The effects of logging on reptiles and amphibians of tropical forests. In: Fimbel RA, Grajal A, Robinson J (Eds) The Cutting Edge. Columbia University Press, New York, 239–260.

Vitt LJ, Colli GR, Caldwell JP, Mesquita DO, Garda AA, França FGR (2007) Detecting variation in microhabitat use in low-diversity lizard assemblages across small-scale habitat gradients. Journal of Herpetology 41: 654–663. http://dx.doi.org/10.1670/06-279.1

Wiens JJ, Graham CH, Moen DS, Smith SA, Reeder TW (2006) Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. American Naturalist 168: 579–596. http://dx.doi.org/10.1086/507882

Wilson LD, Johnson JD, Mata-Silva V (2013a) A conservation reassessment of the amphibians of Mexico based on the EVS measure. Amphibian and Reptile Conservation 7: 97–127.

Wilson LD, Mata-Silva V, Johnson JD (2013a) A conservation reassessment of the reptiles of Mexico based on the EVS measure. Amphibian and Reptile Conservation 7: 1–47.

Woolrich-Piña GA, Ponce P, Loc-Barragán J, Ramírez-Silva JP, Mata-Silva V, Johnson JD, García-Padilla E, Wilson LD (2016) The herpetofauna of Nayarit, Mexico: composition, distribution, and conservation. Mesoamerican Herpetology 3: 376–448.

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RESEARCH ARTICLE

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Effect of climate change on halophytic grasslands loss and its impact in the viability of *Gopherus flavomarginatus*

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Abstract

The decrease of the habitat is one of the main factors that affect the survival of *G. flavomarginatus*. This study assesses the halophytic grasslands loss over a period of 30 years in the distribution area of the Bolson tortoise and the effects of climate change on the habitat suitability of these grasslands and its possible impact on this tortoise. Grassland loss was assessed by an analysis of symmetric differences and the habitat suitability model was carried out by the method of overlapping layers raster. Our results showed a grassland loss of 63.7%; however, our current habitat suitability model points out that much of the grassland loss has occurred where the environmental conditions are suitable. These results suggest that anthropic activity is a main factor in the habitat disturbance in the study area. Likewise, the models for years 2050 and 2070 under the criteria RCP 2.6, RCP 4.5, RCP 6.0, suggest that anthropic activity will continue be the main cause of the grassland loss. Therefore, considering the association between the Bolson tortoise and grassland halophyte *Hilaria mutica*, which comprises around 60% of its diet, the viability of the Bolson tortoise depends largely on strategies aimed at protecting the soil that allow the presence of this grassland.

Keywords

Gopherus flavomarginatus; spatial distribution; climate change; halophytic grasslands

Introduction

Climate influences plant and animal distributions due to their requirements related to temperature and humidity (Parmesan and Yohe 2003; Root et al. 2005; Walther et al. 2005; Lavergne et al. 2006). It has been documented that when climatic factors are extreme, these can exceed the level of tolerance of species, preventing the optimal expression of their life cycles (Gutiérrez and Trejo 2014). Each species has a tolerance interval to diverse environmental factors (Walther et al. 2002; Hardy 2003; Dawson and Spannagle 2009); therefore, its distribution depends on their fundamental niche and their biological interactions (Pearman et al. 2008).

Climate change and change of land use are two of the factors that most affect natural systems (Burroughs 2001; Shafer et al. 2001; Iverson et al. 2008; Harsch et al. 2009; IPCC 2014). The effect of the climate change is more severe on arid and semiarid ecosystems than on humid and semihumid ecosystems (Grime et al. 2008). Thereon, it has been mentioned that facing loss of vegetation of the arid zone, the presence and animal behavior that feed on desert plants could be modified, generating a decrease in the distribution area and in size of their populations (Gandiwa and Zisadza 2010). The effects of the transformation of the vegetation, however, are not uniform for all animal species (Fahrig 2003). Species' response to environmental change will be determined by their physiology (climatic tolerance), morphology (i.e., body size), ecology (feeding habits, habitat selection; nesting sites), dispersal capacity and behavioral characteristics (foraging time, general activity). Therefore, there are species with negative responses by decreasing its abundance and/or its distribution, as well local extinction (Midgley et al. 2007), and other species with positive responses reflected in increasing their abundance and expanding their distribution (Stotz et al. 1996; Thomas et al. 2004; Moritz et al. 2008; Lara et al. 2012).

To assess the effect of the climate change on species distribution, ecological niche modeling has been used employing different environmental variables and mathematical algorithms that try to simulate the climate niche of a species and represent it geographically on a map (Parmesan 2006; Mckenney et al. 2007). In most of the studies, on large spatial scales, only climatic variables have been used for predicting spatial distribution of the species (Araújo and Peterson 2012; Anadón et al. 2015). In some cases, dealing with local spatial scales, soil and orography variables have been included (Guisan and Hofer 2003; Pearson et al. 2004; Anadón et al. 2007; Marini et al. 2010; Kreakie et al. 2012), for example, the dependence of herbivores specialized on some plants (Kissling et al. 2007). Nevertheless, it is very difficult to determine spatial data of biological interactions; and for this reason the studies where the interactions are used to assess the distribution area of the species are very scarce (Pearson and Dawson 2003).

Chihuahuan Desert grasslands provide important resources as habitats and food for sustaining a very rich animal diversity (Vickery et al. 1999). However, the degradation of grasslands is one of the main causes of biodiversity loss on a global scale

Figure 1. *Gopherus flavomarginatus* and halophytic grassland *Hilaria mutica*.

(Gavilán 2008). Given this situation, endemic or native species are the most vulnerable (Contreras-Balderas et al. 2003). *Gopherus flavomarginatus* is an endemic tortoise species of the Bolson of Mapimí zone of the Chihuahuan Desert in the north-central México (Figure 1). The Bolson tortoise is considered vulnerable by IUCN Red List (2017). This species inhabits halophytic grasslands of *Hilaria mutica* on which it feeds, presenting an apparently mandatory association (Aguirre et al. 1979). Therefore, there exists a close interaction between the presence of the grassland and that of the tortoise.

Historically, the Bolson tortoise was distributed from the southwestern USA to the center of México. However, it is currently confined to the area known as the Bolson of Mapimí (Lemos-Espinal and Smith 2007). Considering the low dispersal capacity of the Bolson tortoise and its dependence on the halophytic grass *H. mutica*, a reduction of this grassland, brought about by climate change in the Bolson of Mapimí, would be expected having a strong impact on the viability of the tortoise. Therefore, the goals of this study are: (i) to estimate the change in halophytic grasslands from 1980-2013 period on the current distribution range of *G. flavomarginatus*, (ii) to estimate the projected effect of climate change for the years 2050 and 2070 on the distribution of halophytic grasslands in the Chihuahuan Desert, and (iii) to assess the possible impact of the halophytic grasslands changes on the viability of *G. flavomarginatus*.

Materials and methods

Study area

The Chihuahuan Desert has an approximate area of 507,000 km^2 and elevations from 800 to 2500 m-asl; it extends from central México northward to southern Texas, Arizona, and New México. The mean annual precipitation varies from 175 to 400 mm. The characteristic vegetation is microphyllous desert scrub, rosette desert scrub, crassicaule desert scrub, and grasslands, among others (Rzedowski 1978). About 80% of the soils are derived from calcareous materials (Sutton 2000). Halophytic grasslands of *H. mutica* are distributed throughout the Chihuahuan Desert, whereas the tortoise occurs only in the central zone, in the region known as Bolson of Mapimí, where the Mapimí Biosphere Reserve is located (Lemos-Espinal and Smith 2007).

Zonification of the distribution area of the Bolson tortoise

Sixty one records of *G. flavomarginatus* were identified, with these points we delimited a Minimum Convex Polygon (MCP) of 15,895.5 km^2 that represents the distributional area of the Bolson tortoise. This polygon was zoned according to the densities of the geographic points using the clustering K-means method (Software CrimeStat V. 3.2, 2009).

Influence of the environmental factors on distribution of halophytic grassland

In order to identify loss and gain areas of halophilic grasslands (1980–2013) we used a symmetric difference analysis (Software ArcMap V. 10.1; ESRI 2012). The analysis was performed by using a quadrant of 32,300 km^2 (MCP2) product of add a buffer zone of 10 km around the perimeter of MCP. To this quadrant was added information of land use and vegetation distribution (INEGI 1991, 2013). Likewise, we provided current environmental data (19 climatic layers) with a spatial resolution of 2.5 minutes (~5 km^2), obtained from Worldclim (Hijmans et al. 2005); The bioclimatic variables of Worldclim reflect aspects of temperature and precipitation and have been used successfully for niche models (Davis et al. 2008; Jezkova et al. 2009).

Subsequently, within the area MCP2 were settled 232 quadrants out of 100 km^2, each one. In each quadrant we added the corresponding value for each bioclimatic variable, as well as the information of presence and absence of the halophytic grasslands. In order to identify the bioclimatic variables that explain the presence and absence of the halophytic grasslands in the study area, was used an analysis of discriminant factors (canonical) under the generalized linear model. This analysis was performed using the library "MASS" (Venables and Ripley 2002) in the software R (version 3.1.3).

Habitat suitability models

For modeling the habitat suitability of halophytic grasslands under current climatic conditions in the Chihuahuan Desert, we used the retained bioclimatic variables in the discriminant analysis. The selected variables were annual mean temperature, mean diurnal range, minimum temperature of the coldest month, annual precipitation, and precipitation of wettest quarter, as well as substrate texture data (INEGI 2004). Based on these variables we performed an analysis of frequencies with the purpose of obtaining the climatic profile (maximum and minimum) of the halophytic grasslands. Later, the habitat suitability was modeled using an Additive Overlay Analysis of layer raster method (ArcMap V. 10.1), which delimits the potential habitat suitability of one species based on knowledge of its climatic profile. To these are given a weighting according to the importance of the layer and abundance of the points on the polygon, and the cells are extracted from the raster layer by a logical search. Outlet layers contain only the values of the cells or pixels extracted from the input layer and output layers that were used in the superposition processes.

The same climatic profile was used for modeling habitat suitability for the scenario of the climatic change to 2050 and 2070 in the Chihuahuan Desert. We used data as scenarios of the climatic change corresponding to the extrapolated with Beijing Climate Center Climate System Model (BCC-CSM1-1, this was chosen at random from a group of 19 climate models) for the years 2050 and 2070 under different Representative Concentration Pathways (RCP): RCP 2.6 = +2.6 W/m^2, RCP 4.5 = +4.5 W/m^2, RCP 6.0 = +6.0 W/m^2, and RCP 8.5 = +8.5 W/m^2 were used as scenarios of the climatic change. Under the scenario RCP 2.6 a minor intensity of the effects of the climate changes is expected, while with the scenario RCP 8.5 the intensity will be greater (Weyant et al. 2009). The model additive overlay of layer raster predict habitat suitability as a function of environmental variables and species occurrence data, this habitat suitability is represented by a scale ranging from 0 (low suitability) to one (high fitness), we used a cut-off point of 0.5.

The emergence of new technologies and recent assumptions about socioeconomic development, as well as observations of environmental factors such as land use and land cover change have been considered in this new generation of scenarios (Moss et al. 2010; Rogelj et al. 2012; van Vuuren 2012). The RCPs explicitly explore the impact of different climate policies in addition to the no-climate-policy SRES scenarios (van Vuuren et al. 2011b) and provide an important reference point to investigate the potential implications of climate change on ecosystems (van Vuuren et al. 2011a).

For the validation of the model were used the zones with presence of halophytic grasslands in the Chihuahuan Desert reported by the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) (2015).

Exchange rate

To assess the climate change impact on the habitat suitability of the halophytic grasslands we obtained the percentage change for each scenario using the following formula (Gutiérrez and Trejo 2014):

% of change = $[(S1 - S0)/S0]*100$,

Where:
$S0$, is the total surface of the study area, according to the base scenario.
$S1$, is the total surface occupied in the study area under change conditions.

Results

Three zones in the distribution area of *G. flavomarginatus* were identified, these zones were classified as "A" with 2,649.99 km^2, "B" with 5,472.21 km^2, and "C" with 2,657.11 km^2 (Figure 2). The zone "A" coincides with the polygon of the Reserve of Mapimí Biosphere, and it is the lesser extension of the three identified zones (Figure 2). For MCP2 (quadrant of 32,300 km^2), in a period of 30 yrs, we recorded a halophytic grasslands loss of 1,286.66 km^2 and a gain of 518 km^2 (Figure 2); therefore, for the year 2013 the extension of the halophytic grasslands in the MCP2 was 1350.44 Km^2. The transformed Wilks value, obtained from discriminant analysis shows that the null hypothesis should be rejected ($\lambda = 0.834$, $x^2 = 56.478$, g.l. = 18, p = 0.000); therefore, the two discriminant groups (presence and absence) should be considered as distinct.

The current model habitat suitability identifies the greatest part of the localities where halophytic grasslands had been reported in the Chihuahuan Desert (CONABIO 2015) (Table 1, Figure 3); the projected habitat suitability for Chihuahuan Desert shows that habitat suitability loss was relatively low for the scenarios RCP 6.0, RCP 4.5, and RCP 6.0 for the years 2050 and 2070 (Table 2, Figure 3). However, under the scenario RCP 8.5 for the years 2050 and 2070 the models of habitat suitability show a loss of 43.18% and 89.3%, respectively. Considering the scenario RCP 8.5 for year 2050, halophytic grasslands only it remains in B zone; while for year 2070 disappear completely the habitat suitability in the current distribution area of the Bolson tortoise (Table 2, Figure 3). Under the scenario RCP 8.5 for 2050 and 2070, the loss of habitat suitability for halophytic grassland was much higher than for the rest of the scenarios (Table 2). In RCP 2.6 we obtained the lower estimates of reductions of habitat suitability for grasslands.

Discussion

The results of this study show that halophytic grassland loss in the current distribution area of *G. flavomarginatus* has been a continuous process, in as much as in a period of

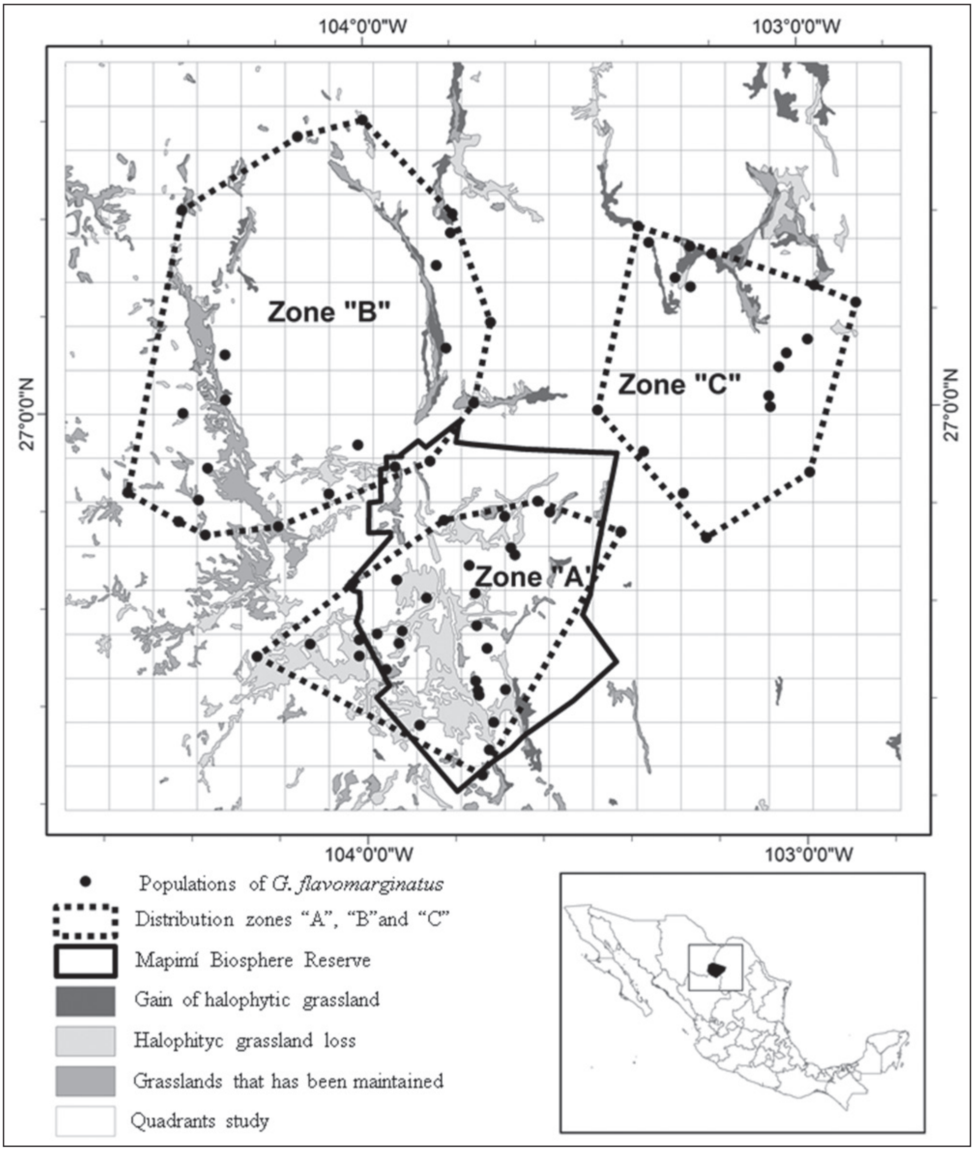

Figure 2. Distribution of gain and loss of the halophytic grassland in an area of 32,300 km^2. Black spots show populations of *G. flavomarginatus*; dotted lines show distribution zones "**A**", "**B**" and "**C**" of the species; the black line indicates the Mapimí Biosphere Reserve; dark grey color shows the zones with gain of halophytic grassland; light grey color shows the zones of halophytic grassland loss; medium grey color shows areas with grasslands that has been maintained; the grid make reference to squares of 100 km^2 in the study area.

30 years its reduction has been 63.7%, with the zone "A" being the most affected. In this context, halophytic grasslands loss for the Chihuahuan Desert has been attributed to the climatic change and to the anthropic factors (e.g., agriculture and cattle; Vavra et al. 1994; Archer et al. 1995; Hodgson and Illius 1996; Aguirre et al. 1997; Moleele

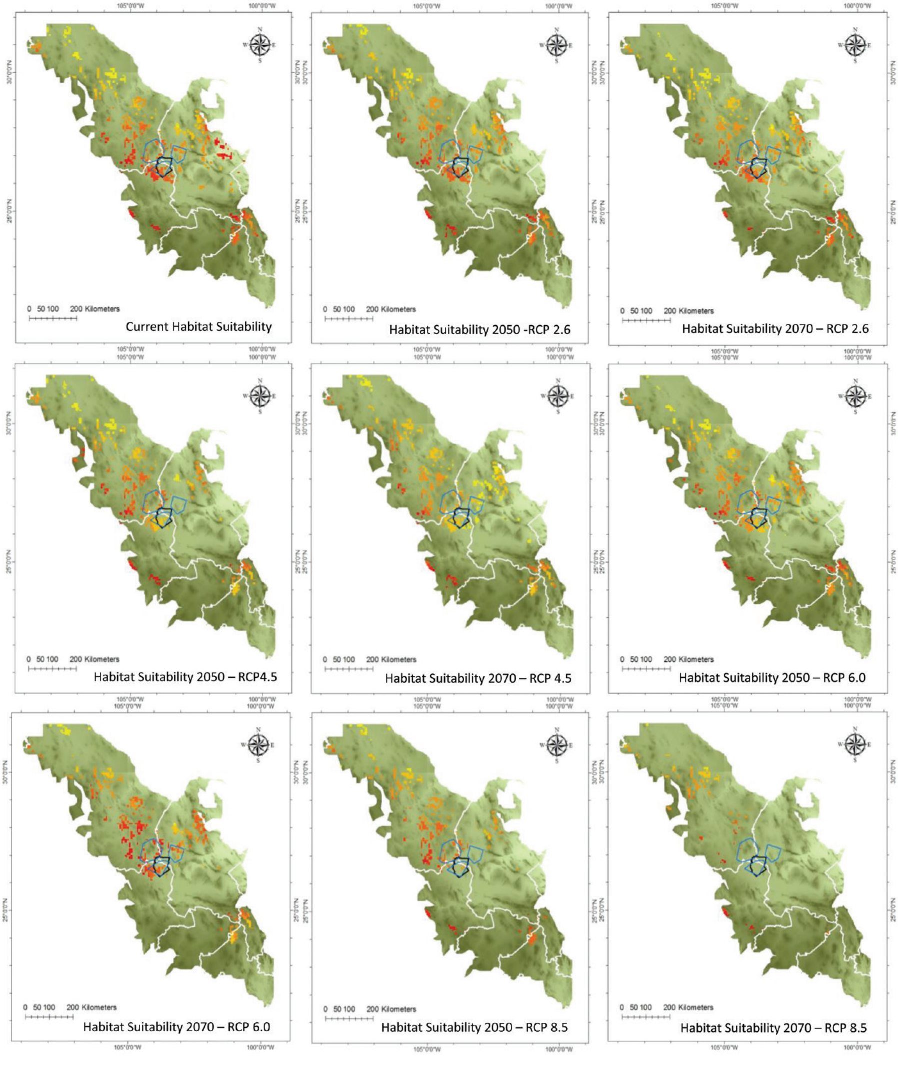

Figure 3. Habitat suitability models of the halophytic grasslands projected for Chihuahuan Desert. White lines show states boundaries; black lines refer to the Mapimí Biosphere Reserve; blue lines indicate distribution zones of *G. flavomarginatus*.

and Perkins 1998; Van Auken 2000). In this regard, Archer (1994) pointed out that the grassland loss is an event that is happening in arid and semiarid ecosystems worldwide; while Comstock and Ehleringer (1992) and Cook and Irwin (1992) showed that the climate is the main factor to explain the variation in vegetation patterns.

The current habitat suitability model of this study indicates that climatic conditions of the area that showed the highest loss of halophytic grassland inside the known distribution range of *G. flavomarginatus* (zone "A") are appropriate for the presence of this grassland. Data on land use and vegetation presented by Instituto Nacional de

Table 1. Habitat suitability for distribution of *G. flavomarginatus* considering the different climatic scenarios assessed.

Habitat suitability	Zone A	Zone B	Zone C
Current habitat suitability	1,087.99 km^2	999.49 km^2	594.04 km^2
Habitat suitability RCP 2.6-2050	1,087.56 km^2	999.48 km^2	594.02 km^2
Habitat suitability RCP 4.5-2050	1,007.85 km^2	1,027.28 km^2	0 km^2
Habitat suitability RCP 6.0-2050	1,179.83 km^2	1,065.37 km^2	624.11 km^2
Habitat suitability RCP 8.5-2050	143.066 km^2	1,023.241 km^2	0 km^2
Habitat suitability RCP 2.6-2070	1,087.43 km^2	999,46 km^2	593.92 km^2
Habitat suitability RCP 4.5-2070	1,008.61 km^2	1,117.54 km^2	657.39 km^2
Habitat suitability RCP 6.0-2070	921.69 km^2	999.77 km^2	510.25 km^2
Habitat suitability RCP 8.5-2070	0 km^2	25.7 km^2	0 km^2

Table 2. Change rate of the habitat suitability area for halophytic grassland in Chihuahuan Desert considering current and future climatic conditions (2050 and 2070) under concentrations of greenhouse gases RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5.

Current model	Model 2050	Model 2070	Model 2050	Model 2070	Model 2050	Model 2070	Model 2050	Model 2070
	RCP 2.6		RCP 4.5		RCP 6.0		RCP 8.5	
29,715.73	27,413.14	26,133.87	23,414.74	26,644.12	26,401.96	22,390.37	16,288.26	5,546.78
Change rate (%)	-7.74	-12.05	-21.20	-10.33	-11.15	-24.65	-45.18	-81.33

Estadística y Geografía (INEGI 2013) show that zone "A" and its surroundings presents a strong agricultural and cattle impact. Likewise, it has been noted that reduction and fragmentation of the vegetation cover in the Natural Protected Area of Mapimí Biosphere placed inside Zone "A" is caused by overgrazing (CONANP 2006). In this manner, based on this information, it is possible to point out that beyond the influence of the environmental factors in determining the presence or absence of halophytic grassland, anthropic activities are the main factors that are influencing the loss of this grassland in the current distribution area of the Bolson tortoise by causing fragmentation of this corridor route of halophytic grassland among zones A, B, and C.

In this context, it has been documented that changes in vegetal species distribution promote that animal species also modify their behavior and distribution (Gurd et al. 2001; Steffan-Dewenter et al. 2002). However, when individuals of one species are not able to disperse and colonize new areas with suitable habitat quality or do not possess a wide range of physiological tolerance, their extinction is highly likely (Holt 1990; Kattan and Murcia 2003; Brooks et al. 2004; Uezu et al. 2005; Wilcox and Thurow 2006). In this regard, it has been pointed out that this situation is frequently observed in specialist species (Gascon et al. 1999). For example, it has been documented that grassland fragmentation in the Chihuahuan Desert has affected the biological biodiversity causing isolation and reduction in 60% of the bird populations that inhabit grasslands (Desmond et al. 2005). Likewise, in *Cynomys mexicanus*, an endangered mammal and strongly associated with halophytic grassland in the Chihuahuan Desert, it has been seen that the distance among colonies of this species increase with the grassland fragmentation preventing natural dispersal and the interactions of the animals among populations (Yeaton and Flores-Flores 2006).

For the lizard species *Uma exul* and *Uma paraphygas*, it has been reported that their specificity on dune ecosystems and their low dispersal capacity reduce the probability of migration to places where the habitat conditions are suitable to live. These two species show very low genetic variability; therefore, it has been pointed out that these species are in critical condition because of the transformation of their habitat (Gadsden et al. 1993; Gadsden 1997; Ballesteros-Barrera et al. 2007). Likewise, since 1987, in 20 of 50 amphibian species of cloud forest from Monte Verde, Costa Rica, including the endemic Golden Frog (*Incilius periglenes*), as well as species of the *Anolis* genus have disappeared because of habitat fragmentation (Schneider 1999).

Accordingly, considering the association between Bolson tortoise and the halophytic grass *H. mutica* that comprises 60% of its diet (Aguirre et al. 1979), and taking into account the decreased food availability in the environment, the Bolson tortoise tends to reduce its home range (Hoogland 2006). Therefore, its low dispersal ability (Ureña-Aranda et al. 2015), low genetic variability (Ureña-Aranda and Espinosa de los Monteros 2012), and fragmentation and loss of grassland *H. mutica* are the main threats for the Bolson tortoise, because these factors favor isolation of the populations of this tortoise by intensifying the low genetic variability of the species. These conditions promote less resistance to extreme temperatures, drought events, change in food availability, emerging diseases, among other features, thus causing population extinction (Hoelzel et al. 2002; Russello et al. 2004; Zhang et al. 2004).

On the other hand, expectations of climate change for years 2050 and 2070 under scenarios RCP 2.6, RCP 4.5, and RCP 6.0 show a slight decrease in habitat availability for halophytic grassland in the Chihuahuan Desert, zones A and B, however show relative stability. This suggests that fragmentation of halophytic grassland in the range of the Bolson tortoise will depend on the change in land use. Under conditions of a pessimistic scenario (RCP 8.5) change rate of the habitat suitability area for halophytic grassland in the Chihuahuan Desert for years 2050 and 2070 will be of -45.186 and -81.333%, respectively. Under this scenario the viability of the Bolson tortoise is heavily compromised.

In conclusion, viability of the Bolson tortoise will depend on the strategies of protection and the land conservation allowing for the presence of halophytic grassland composed of *H. mutica*. In this regard, conservation programs for the Bolson tortoise and its habitat currently are addressed mainly within the Mapimí Biosphere Reserve; however, according to the available evidence, this zone is strongly affected by anthropogenic factors. Likewise, monitoring programs of the populations and habitat conditions of the Bolson tortoise are performed in an area of 1 km^2 scattered inside the Protected Natural Area (CONANP 2016). Faced with this situation, conservation programs of the habitat are needed for allowing connection of the populations inside and outside the Protected Natural Area. Therefore, we propose protection of the A, B, and C zones and the connections among them, so that in this way genetic interchange among populations can be favored. On the other hand, due to threats of climate change, it is necessary to develop an *ex situ* conservation program for *G. flavomarginatus* as well as the conservation of the area that show a habitat suitability outside the current distribution range of the Bolson tortoise, thinking about reintroduction of the species. Also, it is necessary to point out that the algorithms of potential area of habitat suitability involve a certain level of uncertainty that becomes worse in the projections to simulated scenarios (Pearson et al. 2006). However, we consider that our results provide an early warning about the possible consequences of the current activities on land use and the climate change due to increasing temperature.

Author contributions

Conceptualization: JLBL NPP URM. Formal analysis: JLBL URM. Investigation, writing and editing: JLBL URM NPP GSR ARB. Resources: JLBL URM NPP GSR ARB.

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References

Araújo MB, Peterson AT (2012) Uses and misuses of bioclimatic envelope modeling. Ecology 93: 1527–1539. http://dx.doi.org/10.1890/11-1930.1

Aguirre G, Morafka DJ, Adest GA (1997) Conservation strategies for the Bolson Tortoise, *Gopherus flavomarginatus*, in the Chihuahuan Desert. In: Van Abbema J (Ed.) Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles-An International Conference. Conference. New York Turtle and Tortoise Society, New York, 333–338.

Anadón JD, Graciá E, Giménez A, Fahd S, Fritz U (2015) Individualistic responses to climate changes: niche differentiation promotes diverging Quaternary range dynamics in the subspecies of *Testudo graeca*. Ecography 38: 956–966. https://doi.org/10.1111/ecog.01163

Anadón JD, Giménez A, Martínez M, Palazón JA, Esteve MA (2007) Assessing changes in habitat quality due to land use changes in the spur-thighed tortoise *Testudo graeca* using hierarchical predictive habitat models. Diversity and Distributions 13: 324–331. https://doi.org/10.1111/j.1472-4642.2007.00343.x

Aguirre G, Adest GA, Recht M, Morafka DJ (1979) Preliminary investigations of the movements, thermoregulation, population structure and diet of the Bolson tortoise (*Gopherus* *flavomarginatus*) in the Mapimí Biosphere Reserve, Durango, México. Proceedings Desert Tortoise Council 149–165.

Archer S, Schimel DS, Holland EA (1995) Mechanisms of shrubland expansion: land use, climate, or CO2? Climatic Change 29: 91–99. http://dx.doi.org/10.1007/BF01091640

Archer S (1994) Woody Plant Encroachment into Southwestern Grasslands and Savannas: Rates, Patterns and Proximate Causes. In: Vavra M, Laycock W, Pieper R (Eds) Ecological Implications of livestock herbivory in the West. S.R.M. Denver, CO, 13–68.

Ballesteros-Barrera C, Martínez-Meyer E, Gadsden H (2007) Effects of land-cover transformation and climate change on the distribution of two microendemic lizards, genus *Uma*, of Northern México. Journal of Herpetology 41: 733–740. https://doi.org/10.1670/06-276.1

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. BioScience 54: 677–688. https://doi.org/10.1641/0006-3568(2004)054[0677:EOIAPO]2.0.CO;2

Burroughs WJ (2001) Climate change a multidisciplinary approach. Cambridge University Press, London: 248. https://doi.org/10.1017/S0016756803338129

Comstock JP, Ehleringer JR (1992) Plant adaptation in the Great basin and Colorado Plateau. Great Basin National 52: 195–215. http://scholarsarchive.byu.edu/ gbn/vol52/iss3/1

Contreras-Balderas S, Almada Villela P, Lozano Vilano M, García Ramírez M (2003) Freshwater fish at risk or extinct in Mexico. Reviews in Fish Biology and Fisheries 12: 241–251. https://doi.org/10.1023/A:1025053001155

Cook JG, Irwin LL (1992) Climate–vegetation relationships between the Great Plains and Great Basin. The American Midland Naturalist 127: 316–326. https://doi.org/10.2307/2426538

CONABIO (2015) Comisión Nacional Para el Conocimiento y Uso de la Biodiversidad. http://www.biodiversidad.gob.mx/ecosistemas/images/mapa3_3.jpg

CONANP (2006) Comisión Nacional de Áreas Naturales Protegidas – Programa de conservación y manejo Reserva de la Biosfera Mapimí, México. http://www.conanp.gob.mx / datos_abiertos/DGCD/76.pdf

CONANP (2016) Comisión Nacional de Áreas Naturales Protegidas – Monitoreo de la tortuga del Bolsón (*Gopherus flavomarginatus*) en la Reserva de Biosfera Mapimí. http://www.conanp.gob.mx/programas/pdf/Anexo%202%20Protocolo%206%20RB%20Mapimi.pdf

Davis ED, Koo MS, Conroy C, Patton JL, Moritz C (2008) The California Hotspots Project: identifying regions of rapid diversification of mammals. Molecular Ecology 17: 120–138. https://doi.org/10.1111/j.1365-294X.2007.03469.x

Dawson B, Spannagle M (2009) The complete guide to climate change. Routledge, New York, 394 pp. https://www.amazon.com/Complete-Guide-Climate-Change/dp/0415477905

Desmond MJ, et al. (2005) Habitat associations and conservation of grassland birds in the Chihuahuan Desert Region: two case studies in Chihuahua, México. In: Cartron JL E, Ceballos G, Felger RS (Eds) Biodiversity, ecosystems, and conservation in northern México. Oxford University Press, New York, 439–51.

ESRI (2012) Environmental Scientific Research Institute – ArcGIS 10.1. Redlands, California.

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34: 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Gadsden HE (1997) Autoecología de las lagartijas de arena *Uma paraphygas* y *Uma exsul* (Sauria: Phrynosomatidae) en las dunas del Bolsón de Mapimí. Informe final del Proyecto L173.

Gadsden HE, Méndez de la Cruz FR, Gil-MartÍnez R, Casas-Andreu G (1993) Patrón reproductor de una lagartija (*Uma paraphygas*) en peligro de extinción. Boletín de la Sociedad Herpetológica Mexicana, 5: 42–50. http://sociedad herpetológi camexicana.org.mx/publicaciones/boletin-de-la-shm/1993-vol-5/

Gandiwa E, Zisadza P (2010) Wildlife management in Gonarezhou National Park, southeast Zimbabwe: Climate change and implications for management. Nature and Faune 25: 95–104. http://www.fao.org/docrep/013/am071e/am071e00.pdf

Gascon C, Lovejoy TE, Bierregaard RO Jr, Malcolm JR, Stouffer PC, Vasconcelos HL, Laurance W, Zimmerman B, Tocher M, Borges S (1999) Matrix habitat and species persistence in tropical forest remnants. Biological Conservation 91: 223–229. https://doi.org/10.1016/S0006-3207(99)00080-4

Gavilán RG (2008) La vegetación de alta montaña. In: Redondo M, Palacios M, López F, Santamaría T, Sánchez D (Eds) Avances en biogeografía Universidad Complutense de Madrid, Facultad de Geografía e Historia, Madrid, 165–174.

Guisan A, Hofer U (2003) Predicting reptile distributions at the mesoscale: relation to climate and topography. Journal of Biogeography 30: 1233–1243. https://doi.org/10.1046/j.1365-2699.2003.00914.x

Gurd DB, Nudds TD, Rivard DH (2001) Conservation of mammals in eastern North American wildlife reserves: how small is too small? Conservation Biology 15: 1355–1363. https://doi.org/10.1111/j.1523-1739.2001.00188.x

Gutiérrez I, Trejo E (2014) Efecto del cambio climático en la distribución potencial de cinco especies arbóreas de bosque templado en México. Revista Mexicana de Biodiversidad 85: 179–188. https://doi.org/10.7550/rmb.37737

Grime JP, Fridley JD, Askew AP, Thompson K, Hodgson JG, Bennett R (2008) Long-term resistance to simulated climate change in an infertile grassland. Proceedings of the National Academy of Sciences, USA, 105: 10028–10032. https://doi.org/10.1073/pnas.0711567105

Hardy JT (2003) Climate Change: Causes, Effects and Solutions. John Wiley and Sons, West Sussex, England. http://www.wiley.com/WileyCDA/WileyTitle/productCd-0470850191.html

Harsch MA, Hulme PE, McGlone MS, Duncan RP (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12: 1040–1049. https://doi.org/10.1111/j.1461-0248.2009.01355.x

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965-1978. https://doi.org/10.1002/joc.1276

Hoelzel AR, Fleischer RC, Campagna C, Le Boeuf BJ, Alvord G (2002) Impact of a population bottleneck on symmetry and genetic diversity in the northern elephant seal. Journal of Evolutionary Biology 15: 567–575. https://doi.org/10.1046/j.1420-9101.2002.00419.x

Hodgson J, Illius AW (1996) The ecology and management of grazing systems. CAB International. Wallingford, United Kingdom: 466.

Hoogland LJ (2006) Conservation of the Blacktailed Praired Dog. Saving North America's Western Grasslands. Island Press: 350.https://islandpress.org/book/conservation-of-the-black-tailed-prairie-dog

Holt RD (1990) The microevolutionary consequences of climate change. Trends in Ecology and Evolution 5: 311–315. http://dx.doi.org/10.1016/0169-5347(90)90088-U

INEGI (1991) Instituto Nacional de Estadística y Geografía – Conjunto de datos vectoriales de la carta de uso del suelo y vegetación: escala 1: 250 000. Serie I (continuo nacional). Instituto Nacional de Estadística, Geografía e Informática. http://www.inegi.org.mx/

INEGI (2004) Instituto Nacional de Estadística y Geografía – Conjunto de datos vectorial edafológico: escala 1:250000. Serie II (continuo nacional). Instituto Nacional de Estadística, Geografía e Informática. http://www.inegi.org.mx/

INEGI (2013) Instituto Nacional de Estadística y Geografía – Conjunto de datos vectoriales de la carta de uso del suelo y vegetación: escala 1: 250 000. Serie V (continuo nacional). Instituto Nacional de Estadística, Geografía e Informática. http://www.inegi.org.mx/

IPCC (2014) Intergovernmental Panel on Climate Change – Climate Change 2013: The physical science basis: Working group I contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

IUCN (2017) International Union for Conservation of Nature – IUCN Red List of Threatened Species. http://www.iucnredlist.org/details/9402/0

Iverson LR, Prasad AM, Matthews SN, Peters M (2008) Estimating potential habitat for 134 eastern US tree species under six climate scenarios. Forest Ecology and Management 254: 390–406. https://doi.org/10.1016/j.foreco.2007.07.023

Jezkova T, Jaeger JR, Marshall ZL, Riddle BR (2009) Pleistocene impacts on the phylogeography of the Desert Pocket Mouse (*Chaetodipus penicillatus*). Journal of Mammal 90: 306–320. https://doi.org/10.1644/08-MAMM-A-243.1

Kattan GH, Murcia C (2003) A review and synthesis of conceptual frameworks for the study of forest fragmentation. In: Bradshaw GA, Mooney HA (Eds) How landscapes change: human disturbance and ecosystem fragmentation in the Americas. Springer-Verlag, New York, 183–200. https://doi.org/10.1007/978-3-662-05238-9_11

Kissling WD, Rahbek C, Böhning-Gaese K (2007) Food plant diversity as broad-scale determinant of avian frugivore richness. Proceedings of the Royal Society B 274: 799-808. https://doi.org/10.1098/rspb.2006.0311

Kreakie BJ, Fan Y, Keitt TH (2012) Enhanced migratory waterfowl distribution modeling by inclusion of depth to water table data. PLoS ONE 7(1). https://doi.org/10.1371/journal.pone.0030142

Lara C, Feria-Arroyo TP, Dale J, Muñoz J, Arizmendi MC, Ornelas JF (2012) Potential effects of the climate change in the distribution of hummingbirds: a study case with hummingbirds from the genus *Amazilia* and *Cynanthus*. Ornitologia Neotropical 23: 57–70.

Lavergne S, Molina J, Debussche M (2006) Fingerprints of environmental change on the rare Mediterranean flora: a 115-year study. Global Change Biology 12: 1466–1478. https://doi.org/10.1111/j.1365-2486.2006.01183.x

Lemos-Espinal J, Smith H (2007) Anfibios y reptiles del estado de Chihuahua, México. UNAM-CONABIO, México, 550 pp.

Levine N (2009) CrimeStat: a spatial statistics program for the analysis of crime incident locations, version 3.2. Ned Levine and Associates, Houston, TX, and the National Institute of Justice, Washington, DC.

Marini MÂ, Barbet-Massin M, Lopes LE, Jiguet F (2010) Predicting the occurrence of rare Brazilian birds with species distribution models. Journal of Ornithology 151: 857–866. https://doi.org/10.1007/s10336-010-0523-y

McKenney DW, Pedlar JH, Lawrence KM, Campbell KL, Hutchinson MF (2007) Potential impacts of climate change on the distribution of North American trees. BioScience 57: 939–948. https://doi.org/10.1641/B571106

Midgley GF, Thuiller W, Higgins SI (2007) Plant species migration as a key uncertainty in predicting future impacts of climate change on ecosystems: progress and challenges. In: Canadell JG, Pataki DE, Pitelka LF (Eds) Terrestrial Ecosystems in a Changing World. Springer, New York, 129–137. https://doi.org/10.1007/978-3-540-32730-1_11

Moleele NM, Perkins JS (1998) Encroaching woody plant species and boreholes: is cattle density the main driving factor in the Olifants Drift communal grazing lands, south-eastern Botswana? Journal of Arid Environments 40: 245–253. https://doi.org/10.1006/jare.1998.0451

Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science 322: 261–264. https://doi.org/10.1126/science.1163428

Moss R, et al. (2010). The next generation of scenarios for climate change research and assessment. Nature 463: 747–756. https://doi.org/10.1038/nature08823

Pearson PN, et al. (2004) Paleogene and Cretaceous sediment cores from the Kilwa and Lindi areas of coastal Tanzania: Tanzania Drilling Project Sites 1–5. J. Journal of African Earth Sciences 39: 25–62. https://doi.org/10.1016/j.jafrearsci.2004.05.001

Pearson RG, et al. (2006) Model-based uncertainty in species range prediction. Journal of Biogeography 33: 1704–1711. https://doi.org/10.1111/j.1365-2699.2006.01460.x

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12: 361–371. https://doi.org/10.1046/j.1466-822X.2003.00042.x

Parmesan C (2006) Ecological and evolutionary response to recent climatic change. Annual Review of Ecology, Evolution, and Systematics 37: 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Pearman PB, Guisan A, Broennimann O, Randin CF (2008) Niche dynamics in space and time. Trends in Ecology and Evolution 23: 149–158. https://doi.org/10.1016/j.tree.2007.11.005

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37–42. https://doi.org/10.1038/nature01286

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Rzedowski J (1978) Vegetación de México. Limusa, México.

Rogelj J, Meinshausen M, Knutti R (2012) Global warming under old and new scenarios using IPCC climate sensitivity range estimates. Nature Climate Change 2: 248–253. https://doi.org/10.1038/nclimate1385

Root TL, MacMynowski DP, Mastrandrea MD, Schneider SH (2005) Human-modified temperatures induce species changes: joint attribution. Proceedings of the National Academy of Sciences, USA 102: 7465–7469. https://doi.org/10.1073/pnas.0502286102

Russello MA, Gladyshev E, Miquelle D, Caccone A (2004) Potential genetic consequences of a recent bottleneck in the Amur tiger of the Russian far east. Conservation Genetics 5: 707–713. https://doi.org/10.1007/s10592-004-1860-2

Shafer SL, Bartlein PJ, Thompson RS (2001) Potential changes in the distribution of western North America tree and shrub taxa under future climate scenarios. Ecosystems 4: 200–215. https://doi.org/10.1007/s10021-001-0004-5

Schneider SH (1999) Amphibian declines in the cloud forest of Costa Rica: responses to climate change? USGCRP Seminar, 29 September 1999.

Stotz DF, Fitzpatrick JW, Parker III TA, Moskovits DK (1996) Neotropical birds: ecology and conservation. The University of Chicago Press, Chicago. EE.UU.

Steffan-Dewenter I, Munzenberg U, Burger C,Thies C, Tscharntke T (2002) Scale-dependent effects of landscape structure on three pollinator guilds. Ecology 83: 1421–1432. https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

Sutton A (2000) El Desierto Chihuahuense, nuestro desierto. Fondo Mundial para la Naturaleza. http://www.pronatura.org

Thomas CD, et al. (2004) Extinction risk from climate change. Nature 427: 145–148. https://doi.org/10.1038/nature02121

Uezu A, Metzger JP, Vielliard JM (2005) The effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. Biological Conservation 123: 507–519. https://doi.org/10.1016/j.biocon.2005.01.001

Ureña-Aranda CA, Espinosa de los Monteros A (2012) The genetic crisis of the Mexican Bolson tortoise (*Gopherus flavomarginatus*: Testudinidae). Amphibia-Reptilia 33: 45–53. https://doi.org/10.1163/156853811X621508

Ureña-Aranda, CA, Rojas-Soto O, Martínez-Meyer E, Yáñez-Arenas C, Landgrave Ramírez R, Espinosa de los Monteros A (2015) Using Range-Wide Abundance Modeling to Identify Key Conservation Areas for the Micro-Endemic Bolson tortoise (*Gopherus flavomarginatus*). PLoS ONE 10(6): e0131452. https://doi.org/10.1371/journal.pone.0131452

van Vuuren DP (2012) A proposal for a new scenario framework to support research and assessment in different climate research communities. Global Environmental Change 22: 21–35. http://www.sciencedirect.com/science/journal/09593780

van Vuuren DP, Edmonds JA, Kainuma M, Riahi K, Weyant J (2011a) A special issue on the RCPs. Climatic Change 109: 1–4. https://doi.org/10.1007/s10584-011-0157-y

van Vuuren DP, et al. (2011b) The representative concentration pathways: an overview. Climatic Change 109: 5–31. https://doi.org/10.1007/s10584-011-0148-z

Van Auken OW (2000) Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics 31: 197–215. https://doi.org/10.1146/annurev.ecolsys.31.1.197

Vavra M, Laycock W, Pieper R (1994) Ecological implications of livestock herbivory in the West. Society for Range Management, Denver, Colorado. https://www.cabdirect.org/cabdirect/abstract/19940706040

Venables WN, Ripley BD (2002) modern Applied Statistics with S. Fourth Edition. Springer, New York.

Vickery P, Tubaro PP, Silva J, Peterjohn B, Herkert J, Cavalcanti R (1999) Conservation of grassland birds in the Western Hemisphere. Studies in Avian Biology 19: 2–26. https://miami.pure.elsevier.com/en/publications/conservation-of-grassland-birds-in-the-western-hemisphere

Walther GR, Berger S, Sykes MT (2005) An ecological "footprint" of climate change. Proceedings of the Royal Society of London (Series B) 272: 1427–1432. https://doi.org/10.1098/rspb.2005.3119

Walther G, et al. (2002). Ecological responses to recent climate change. Nature 416: 389–395. https://doi.org/10.1038/416389a

Weyant J, et al. (2009) Report of 2.6 versus 2.9 Watts/m^2 RCPP evaluation panel. Integrated Assessment Modeling Consortium. https://www.ipcc.ch/meetings /session30/inf6.pdf

Wilcox BP, Thurow TL (2006) Emerging issues in rangeland ecohydrology: vegetation change and the water cycle. Rangeland Ecology and Management 59: 220–224. http://dx.doi.org/10.2111/05-090R1.1

Yeaton RI, Flores-Flores JL (2006) Patterns of occurrence and abundance in colony complexes of the mexican prairie dog (*Cynomys mexicanus*) in productive and unproductive grasslands. Acta Zoologica Mexicana 22: 107–130. http://www.redalyc.org/pdf/402/40223164008.pdf

Zhang B, Fang SG, Xi YM (2004) Low genetic diversity in the Endangered crested ibis (*Nipponia nippon*) and implications for conservation. Bird Conservation International 14: 183–190. https://doi.org/10.1017/S0959270904000231

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Reconstituting a rainforest patch in southern Benin for the protection of threatened plants

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Abstract

In a twenty-year effort at Drabo, southern Benin, small remnant forests, young fallow and agricultural fields were linked and rehabilitated to develop a 14 ha forest reserve. Forest regrowth was encouraged by managing the natural growth of the local fallow vegetation and by bringing in seeds and other propagules from forest islands of Benin. The succession to shade-tolerant woody forest species of Guineo-Congolian origin at the expense of extra-regional herbs, the co-existence of species with slightly different requirements, and the fate of exotic trees in this natural forest are described. A quantitative assessment of a homogeneous lot indicated 397 trees per ha, with stem diameters >10 cm, 43.7% of them below 20 cm, and a rich undergrowth of 72600 smaller plants per ha, proof of active rejuvenation. Only 4.2% of all plants resulted from the 1041 introduction events, i.e., species per date, mostly of the 253 plant species that were new to Drabo. A total of 635 species were recorded, but 50 did not survive and four are yet to be identified. In June 2016, the total of 581 known living species included 224 trees. Among all plants, 244 hailed from the Guineo-Congolian zone with 17 of Upper Guinean and four of Lower Guinean origin, 113 from the three savannah zones, and 224 were of extra-regional origin. Overall, 72.8% of all woody plants, such as many climbers, all shrubs and trees, were of forest and savanna origin (GC, SG, SZ and S), whereas 70.4% of all herbs came from other regions (At, PAL and Pt). Only 7.0% of all species from the GC zone were in decline; but the further away the plants originated from, the larger the decline in numbers and vigour, up to 64.6% among plants of pan-tropical origin. Particularly pan-tropical herbs became ever rarer, with 80.0% of them declining and confined to the few open spaces along paths. In 2017 the forest harboured 52 threatened species, with threat categories EW, CR, EN or VU on the Red List of Benin, out of 73 IUCN-listed species that could possibly survive in Drabo. Some of these species occur in only one or two other locations in Benin. The biodiversity richness of the rehabilitated forests of Drabo now rivals that of natural rainforest remnants of the region. As the surrounding landscape becomes ever more impoverished because of the high human population and its ever increasing impact, the maintenance of such managed islands of biodiversity is critical. By establishing rare local species from other locations we can compensate for direct human destruction and long-term stochastic loss of species in this highly fragmented landscape where natural seed dispersal is difficult.

Keywords
Benin, sacred forest, threatened plants, IUCN Red List, forest regeneration, Guineo-Congolese semi-deciduous forest

Introduction

During the quaternary Ice Ages, West Africa's rain forests receded to two main refuges situated in today's Côte d'Ivoire/Liberia and southern Cameroon (Figure 1). As climate warmed, forests advanced, though with temporary recessions, but never quite closed the so-called Dahomey Gap in Benin-Togo and south-eastern Ghana, which separates the western Upper Guinean from the eastern Lower Guinean/Congolese forest block (Poorter et al. 2004, Giresse 2008). In present-day Benin, Guineo-Congolese closed semi-deciduous humid forests are limited to tiny patches, most of them so-called sacred forests, which are under threat. The fauna and flora of these forests are composed of species originating from one or the other or both forest blocks, as well as species from different savannah zones (Booth 1958, Robbins 1978, UICN 1996, Sinsin and Kampmann 2010, Neuenschwander et al. 2011).

In a highly populated region with sometimes over 250 people per km^2 (INSAE 2013) and embedded in an agricultural landscape and human-induced so-called derived savannah (Paradis and Houngnon 1977, Mama et al. 2014), these forests are islands of high biodiversity. Covering 0.02% of the national territory, they harbour 20% of all plant species and 64% of the highly threatened plants, but are mostly outside established nature reserves (Adomou et al. 2011). Their protection has been described as the highest priority for nature conservation in Benin (Neuenschwander et al. 2011). Many of these forests are severely degraded in terms of structure and species diversity, which calls for rehabilitation measures. Apart from the detailed study of Adomou (2005), only short-term mapping of the flora and rapid surveys through interviews have been conducted (Adjanohoun et al. 1989, Sokpon and Agbo 1999, Nagel et al. 2004, Juhé-Beaulaton 2008, Kokou et al. 2008, Hèdégbètan 2011, Agbani 2012, CERF Bénin 2013).

Here we describe a 20-year effort to link up tiny forest fragments and to rehabilitate them through selective management of former farm and fallow land by encouraging forest regrowth and introducing plants from other forest islands of southern Benin. The management of this reconstituted, biodiversity-rich forest with its most important inhabitants, the critically endangered, endemic red-bellied monkey, *Cercopithecus erythrogaster* (Cercopithecidae) and the interactions with the villagers have already been described and compared with management in other forest sites (Neuenschwander et al. 2015).

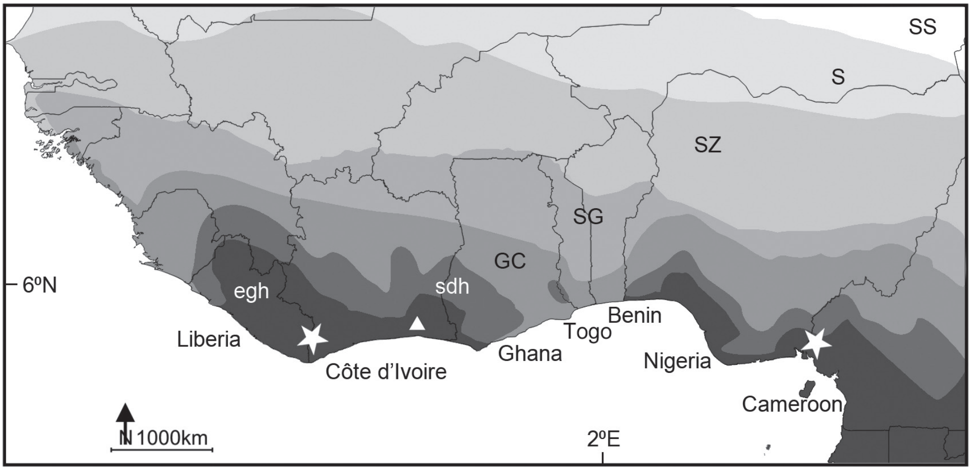

Figure 1. Map of West Africa with ecological zones: SS Sahelo-Sahara, S Sahel savannah, SZ Sudan savannah, SG Guinea savannah, GC Guinea-Congolian forest with closed sdh semi-deciduous forest, egh evergreen forest, asterisks Upper Guinean and Lower Guinean ice-age refuges, triangle Sikensi block. According to Arbonnier (2000), UICN (1996), Chatelain et al. (2004), Hawthorne and Jongkind (2006), and Adomou (2011).

Material and methods

Overall situation

Ecological zones in West Africa (Figure 1) were delimited using Arbonnier (2000) for the north, UICN (1996), Chatelain et al. (2004), Hawthorne and Jongkind (2006) for the south, and Adomou et al. (2006, 2011) for Benin. The main ice age refuges in western Côte d'Ivoire, today Taï National Park, and western Cameroon, today Korup National Park, are marked. In view of the huge human impact in the region, these zones circumscribe the ecological limits for the corresponding vegetation, rather than showing actual forests.

Within the Guinea-Congolese forest zone, the limits for the vegetation and the outer limits of still existing semi-deciduous and evergreen rainforests are therefore given separately. The site of a detailed study of plant cover (Chatelain et al. 2004) in the 20 × 20 km Sikensi block is indicated.

The Dahomey Gap as shown in Figure 1 has a strong gradient of rainfall, with highest rainfall towards the Nigerian border and lowest rainfall in the Accra Plains in Ghana. In Benin, this gradient is reflected in the distinction of phyto-geographical districts within each ecological zone (Figure 2, Adomou 2011). The Guineo-Congolese zone has two widely separated rainy seasons; further north, there is only one rainy season.

Study site

Drabo Gbo (6°30'N; 2°18'E; ca 60 m asl) (Figure 2) is a village of about 500 inhabitants at the southern edge of the Allada plateau, 30 km north of Cotonou, 12 km from

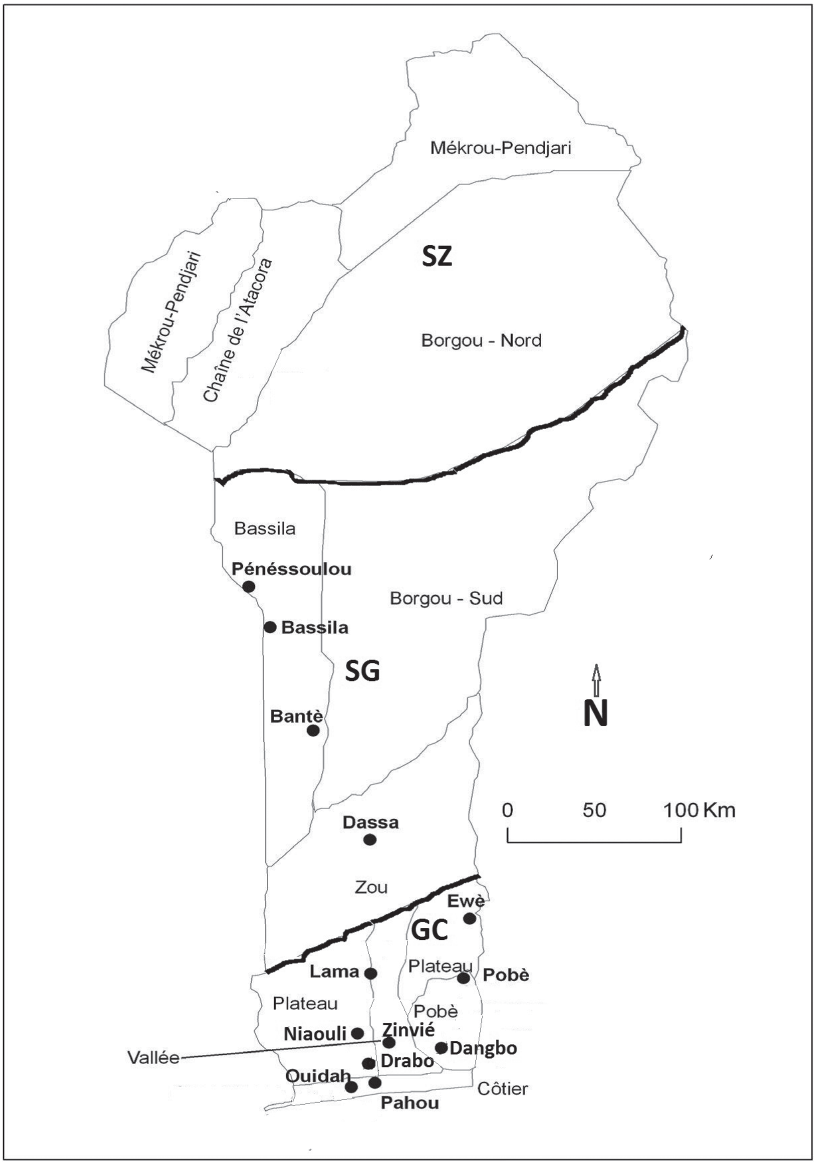

Figure 2. Map of Benin with phyto-ecological zones with GC, SG and SZ as in Figure 1, phyto-geographical districts according to Adomou (2011) in small print.

the spreading town of Calavi. The area has a mean annual rainfall of 1200 mm with two rainy seasons with peaks in May-June and September, and a long dry season from December to February, and a short one from July to August. Variability in rainfall is pronounced. During the period from 1996 to 2016, a maximum of 1815 mm was recorded in 2010 and a minimum of 762 mm in 2000. Daytime temperatures in March-April reach 35 °C, rarely up to 40 °C, and minimum temperatures in January

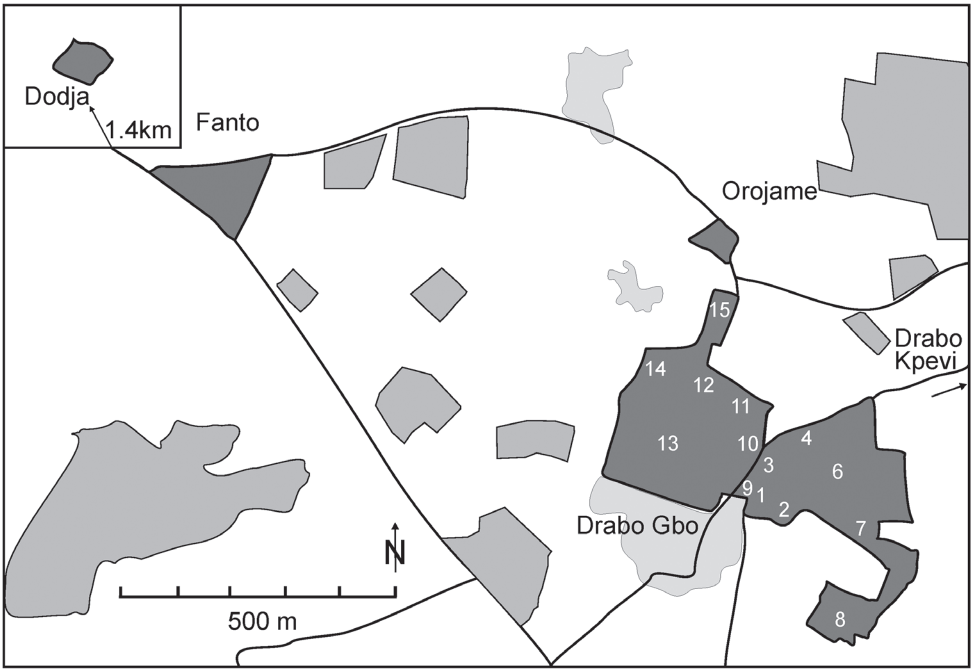

Figure 3. Map of Drabo forests with year of purchase and start of forest management, major clearings: **1** nursery-garden 1997 (house constructed 1997-1998) **2** papa-garage 1999, 2000 **3** Lissanou 1999–2003 **4** mill 2000 **5** Gaston part of Cooun cleared in 2010 **6** Cooun 2001 **7** corridor-Dansou 2004, 2010 **8** Emile 2001–2007 partly cleared 2012 **9** 'Maison de Jeunesse' (MdJ house constructed 2005) 1998, cleared in 2013 **10** Tofinou 1998-2000 **11** Pierre 1999–2001 **12** Kakpo 2004 **13** Grande Forêt 1996, local fire in 2012 **14** AgoXwè 2000–2003 **15** Corridor north 1998, 2002–2003, Orojamè 1998, Fanto 1998–2000, partly cleared 2014, Dodja 2011, partly cleared 2016. Natural forests grey with border line, wood lots light grey with border line, compact villages light grey, unsurfaced roads as lines.

are 20 °C, rarely down to 15 °C during "Harmattan" periods, when a dust-laden wind from the Saharan desert brings cooler night-time temperatures. The study site has a deep lateritic soil. One small lot, called "Emile" in Figure 3, is sandy. The water table throughout is at 25 m depth below the soil surface.

The "Monkey Sanctuary of Drabo Gbo" (Figure 3, centre of map: 6°30.28'N; 2°17.77'E) was founded in 1995 when the first author bought 2.5 ha of teak forest and agricultural land from the elders of Drabo Gbo. The study site was assembled from 25 single lots of different sizes, most of them agricultural fields or recently fallowed land, bought between 1995 and 2005 (for year of purchase of each lot see legend of Figure 3). A small house in the forest and a house for the community called "Maison de Jeunesse" (MdJ), situated on an adjacent triangle of land, were constructed in 1997/98 and 2005, respectively. For some lots, full registration with title deeds has not yet been possible. In January 2014, most of this land was donated by the first author to the International Institute of Tropical Agriculture (IITA) as a site for biodiversity studies. Today there are 14 ha of land that has been managed for forest regrowth from agricultural fallow or teak plantation over 10 to 20 years, as well as tiny sacred forests, like Orojamè (0.8 ha) and Dodja with its old growth forest (0.7 ha). They are adjacent to the village of Drabo Gbo and the smaller villages of Drabo Fanto and Dodja.

History of the land

Speed, quality and abundance of regrowth depend much on the previous occupation of the land (Stanturf et al. 2012, Chazdon 2014). The first author's residence on this site since twenty years offered numerous opportunities for informal interviews with the elders, most of them illiterate farmers, in order to tap into the oral history, which in most families was very much alive.

Management

A flimsy fence of concrete poles, which support five lines of barbed wire, surrounds most of the forest lots; however, effective protection is provided by the "vodun adogba" , i.e., by traditional cults to which the first author has been initiated. Interactions with the surrounding population were described in detail in Neuenschwander et al. (2015), among others that no gathering of fire wood and medicinal plants is allowed.

Management consists of freeing trees from an excessive burden of climbers and maintaining small paths. Exotic timber species, such as *Cassia siamea, Acacia auriculiformis* and *Tectona grandis* (teak), are cut on demand by villagers, but under the supervision of the owner. Among the indigenous commercially important species, oil palm (*Elaeis guineensis*) is by far the most important. On demand, its fruits are collected where easily accessible. During successive fallow cycles, this indigenous species had been protected and enriched to a degree where in many places areas of up to 0.5 ha were so densely stocked that all other vegetation was suppressed. Cutting these oil palms produced sunlit habitats, which triggered the emergence of pioneer trees and offered open space for planting young trees. These were sometimes shaded by cut palm leaves until full rooting was achieved.

Introducing trees, shrubs and lianas from other forests

During the twenty-year period of establishing the forest, numerous collecting trips were made to other patches of forest in southern Benin. Plant material was collected mainly in the following locations (Figure 2): Forest pockets (<1 ha each) near Drabo Gbo and nearby villages; a community forest in Lanzron (50 ha) east of Zinvié in the Ouémé Valley, which is inundated from August to November; the "Forêt de la Panthère" (1.4 ha) of Zinvié (for management of the Lanzron and Zinvié forests see

Neuenschwander et al. 2015); the forest on the national agricultural research station of Niaouli (170 ha), where collections were made along public paths to the small, local stream and beyond; the "Forêt de Kè" at Dangbo (2 ha) bordering swampland; the forest of Ahozon near Pahou (150 ha natural forest), which is the last remaining coastal forest between Lagos and Accra, now under the supervision of the national forest services; the forest of Pobè (about 115 ha) on land of the national oil palm research institute, with a small river; the forest of Ewè (150 ha), a rich but unprotected forest contested by two rival communities and under threat of disappearing completely; the natural forest of the "Noyau Central" of the Lama forest (2000 ha), which is the largest dry type rainforest of Benin, locally inundated and supervised by the managers of the surrounding teak plantations and the official forest station; the community forest of Tobè near Koko, West of Bantè (350 ha), in the Guinea Savannah, which is controlled by the local community and supported by an NGO; the forest of Pénéssoulou still further north; plus exchanges of plants with the Botanic Garden of the University of Abomey-Calavi. With the exceptions of Tobè and Pénéssoulou, the flora of these sites belongs to different phyto-districts of the Guineo-Congolese semi-deciduous forest zone (Adomou 2011).

Most collecting expeditions were conducted in the main rainy season to benefit from conditions favourable for transplanting. To facilitate establishment at Drabo, plants, seeds, or cuttings were first held in a 50 m^2 nursery in open forest near the house, where they could be provided with additional shade if needed, water, and mulch. Most plants remained there for up to a year, awaiting the next significant rains. Recalcitrant seeds were scarified or treated with hot water. Some plants were planted out directly into particular microhabitats, mostly into 5 ha near the habitation of the owner. Watering and mulching during the first year made it possible that also plants from slightly moister forests could survive in Drabo.

Quantitative assessment of regrowth

On "Cooun" (Figure 3), which has the highest proportion of introduced plants among all rehabilitated forests of this study, a uniform regrowth area of about 4 ha was assessed quantitatively in May 2016 to describe first the general habitus of this 20 year old *Albizia-Antiaris-Blighia* forest with a high proportion of oil palms. Second, the importance of introduced plants was to be estimated. The total number of trees >10 cm diameter on 1000 m^2 (a circle measured out with a string of 17.8 m length) and all species of trees, lianas and herbs on 5 times 10 m^2 (in the centre and on the main circle in all four directions, measured with a string of 1.78 m) were assessed. The procedure was repeated three times from randomly chosen points on the narrow main path. Data about trees from 3000 m^2 and all plants from 150 m^2 were extrapolated to numbers of plants per ha. Tree numbers were grouped in 10 cm-diameter intervals, separately for the three dominant *Albizia* sp., two common *Blighia* sp., *Elaeis guineensis*, all other indigenous trees, and all introduced plants. In the small circles, all plants were determined to species and counted. Trees with diameters >10 cm were separately noted to check for congruence in the data, since the surface of the 15 small circles is 5% of the surface of the three big circles.

Inventory of the flora

To register all plant species, parts of the forest were inspected since 1998 daily for "Cooun" and surroundings, weekly for "Grande Forêt" and surroundings, and monthly for Drabo Fanto and Dodja by PN and/or a local guide. Unknown plants were marked with a yellow plastic band for later identification by AA. First identifications in 1997 and 1998 had been made by the late Prof. Paul Houngnon of the National Herbarium of Benin. Plants were identified by means of Akoègninou et al. (2006) and Hawthorne and Jongkind (2006) and by comparison with specimens in the National Herbarium. Additionally, dead or withering plants were noted. If this condition concerned all or most specimens this species was registered as 'decreasing'.

A list of all species registered in these forests is given as supplementary file. Species from aquatic, semi-aquatic, coastal-sand, or rocky habitats as well as horticultural species are excluded because they are not part of the natural flora of Drabo and, where present, survived only under special conditions, i.e., in pots or concrete ponds. The supplementary file lists:

- Taxa (Pteridophytes as 1Pteri, Gymnosperms as 2Gym, Monocotyledons as 3Mono, Dicotyledons as 4Dicot, and non-identified as 5nonid.
- Plants are described as parasites/epiphytes, herbs, climbers, shrubs or trees based on the description in Akoègninou et al. (2006) and–where different growth forms exist–with the habitus they show in Drabo. Species that are either new or not included in this flora are marked. Family names follow taxonomic revisions (APG I 1998, for least differences with Akoègninou et al. 2006).
- Chorology according to Adomou et al. (2010, 2011) and Akoègninou et al. (2006): The origin of the species is indicated as follows (Figure 1): GC Guineo-Congo forest species that are distributed across the Upper and Lower Guinean and into the Congolese zone east to Sudan, Uganda, Kenya, GO Upper Guinea forest species from west of the Dahomey Gap with an eastern limit in Benin or nearby Nigeria, GE Lower Guinea forest species from east of the Dahomey Gap with a western limit in Benin, SG Guineo-Sudanian transition zone species, SZ Sudanian savannah species, and S Sahel savannah species. Many species occur in different zones; only their main habitat is indicated. At indicates Afrotropical species with distributions beyond West and Central Africa into Madagascar, PAL Paleotropical and Pt Pan-tropical species, i.e. all species that have penetrated or invaded West Africa from other floral regions, for example Cocos palm. West African species that have similarly spread across the world are indicated by their original zone, for example oil palm.

- The next column indicates the origin of transplanted species (Figure 2, including Ouéga and the IITA campus a few km south of Drabo, Agongbè north of Drabo, Hévié north of Pahou, Avrankou on the Iguidi River near the Nigerian border east of Dangbo, and Tanougou waterfalls outside the Penjari Park in the Sudan savannah) and their location in the study forests (Figure 3), the years of collecting and transplanting, and–separately–in which form, namely seeds, small plants, sticks, they were collected.
- Abundance in 2016 is ranked as follows: 1 = 1–4 plants established; 2 = 5–10 plants; 3 = up to 20 plants; 4 = common species; 5 = abundant species.
- The maximum height of trees of each species was estimated in April-June 2016, taking into account all study forests. For most species, biggest trees were found in Drabo; in addition, especially big specimens from Dodja (Do), Fanto (Fa) or Orojamè (Or) were indicated.
- The population tendency was roughly estimated as s = stable, i = increasing, d = decreasing. Where necessary, Cut or Lost (**L** = lost by July 2016) were indicated.
- Red List status was given according to Neuenschwander et al. (2011) based on IUCN criteria as NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, EW = extinct in the wild in Benin. All other species were considered as Least Concern because they are not threatened or have not been assessed. In the evaluation of threatened species, NT-species were excluded.
- Suspected reasons for difficulty in establishment were given as: - recalcitrant seeds, which were sometimes treated with hot water or by scarifying, - drought, i.e., temporarily too little water, - savannah species, of which we suspect that they do not support transfer to two rainy seasons and are therefore not capable of reaching the coast, - medicinal use, e.g., roots harvested for increasing male potency.
- The number of samples, which include one to maximum 10 plantlets or seeds per species and date, was indicated.
- Plants originally found on the 14 ha and in their vicinity of a few hundred meters were marked with x. Some of them, if they were rare, were also reproduced and transplanted to other sites.

Percentages were compared by a two-way Chi-square test with correction for continuity.

Results

History in the 20th century

Even before the village of Drabo Gbo had been founded at the end of the 19th century, the area had been under cultivation probably for hundreds of years out of the village of Gbodjo situated at the lagoon near Calavi, with fallow cycles of 15 years or more. Some forests remained untouched and served as sacred forests, like Dodja, the oldest forest in this study. Its *Cola gigantea*, *Celtis milbraedii*, *Blighia sapida* and *Antiaris toxicaria* are probably several hundred years old and reach 40 m. The forest was not touched for perhaps 100 years; but gaps with trees of only 10 m height that are heavily encumbered by lianas indicate that big trees had been cut before the present inhabitants of Dodja can remember. Another sacred forest, Orojamè, was created around a big *Cola* tree about 80 years ago and to date is the central site for the "Oro" cult of the entire area. This site of 0.4 ha was bought in 1999 and increased to about 0.8 ha.

In the former teak forest and another fallow lot, two big *Cola gigantea* trees were included in the newly acquired land. Their preservation was due to a courageous action in the late 1970s by the then "délégué" , who refused political pressure to cut them down because they were reputed to be sites of ghosts. They became islands of biodiversity, from where plants, insects, but also mammals spread to the rest of the developing forest.

About 8 ha, among them "Cooun" where the quantitative study was made, were under forest cover about 50–70 years ago, before the forest was cleared and replaced by maize, teak, *Dialium guineense*, which were stunted to harvest the sweet seeds, or cow "pasture", effectively bush regrowth since the local cows eat only broad leaves, no grass. Since no heavy equipment was ever used, seeds and roots of the previous forest vegetation remained alive. When fallow or crop land was purchased it was mostly devoid of trees. Once cultivation ended, shrubs, some up to man's height, developed into big trees within a few years.

In the past, fire in Fanto was ignited along the edge to catch grass-cutters, a large rodent. Moreover, at Drabo Gbo, six big *Albizia* and *Rhodognaphalon* trees were set on fire by igniting a car tyre at their base. In the same vindictive action in 2013 by villagers, who were enraged because of a local murder, all 65 trees on the triangle of the "Maison de Jeunesse" (MdJ), were cut. This action was ordered by the "Bokonon" (seer), who claimed a bad spirit was located there. The garden of the MdJ has meanwhile been transformed into an ethnobotanical garden. At present, the protection of the forest is good, i.e., no trees are debarked or felled, few lianas cut, no fire is laid, and no hunting is observed, except for some digging-out of ground squirrels or Gambian rats.

Status today

The forests of Drabo are embedded in a landscape of farmland with numerous isolated small houses. The section in Figure 3 covers 2.1 km^2 and shows 80 houses in Drabo Gbo, 16 in Drabo Fanto, 16 on AgoXwè, plus 350 isolated houses on 500 m^2 lots. The surrounding vegetation consists of fallow, which during the period of the study was gradually reduced from a few to zero years. Fields are mostly planted with maize, cassava, or pineapple. Up to now, most land has been sold to people from town by the original owners, who eventually install themselves in this area by building modest one-story houses and grow various fruit trees and bananas. Where construction has not yet started the land is often being abused by the original owners without any consideration to conserve soil fertility. It is therefore often heavily infested with *Imperata cylindrica*. Gradually, big *Cola* and other trees, which were typical of a rich landscape, have been felled and the forest of the present study has meanwhile become an island in an ecologically impoverished surrounding.

Numerous woodlots have been planted with *Cassia siamea, Tectona grandis*, and mostly *Acacia auriculiformis*. The total area of uniform and biodiversity-poor woodlots in Figure 3 is bigger than the 14 ha of forest of the present study. Such lots provide wood for construction and firewood and take the pressure off the reconstituted, biodiverse forest.

Today, trees in Dodja are around 30 m high, with a few up to 40 m. In Orojamè the canopy is at around 20–25 m. In the oldest, selectively managed fallow land, trees reach 20–25 m, but in Drabo Fanto and on "Emile" in Drabo Gbo on sandy soil, the canopy is at only 10–15 m.

In 2016 a quantitative assessment of the vegetation was made in a mixed *Albizia* forest with rich undergrowth on "Cooun ", after 15 years of fallow combined with cow pasture (Figure 4). Among all trees, *Albizia* spp. (half *A. zygia,* ¼ *A. adianthifolia,* ¼ *A. glaberrima*) accounted for 64.7% (N = 119), *Elaeis guineensis* for 13.4%, all other indigenous trees for 19.3%, and the introduced species for only 1.7%. There were 397 trees with diameters >10 cm per ha, resulting in 25.2 m^2 per tree. Young trees with diameters of 10 to 20 cm accounted for 43.7% of all trees. In the small circles, where all plants were identified, a total of 1093 plants were counted, i.e. 72600 plants per ha. Four trees had diameters of >10 cm, which averages out at 267 tree per ha, slightly below the count from the big lots. This rich undergrowth was variously dominated by *Mallotus oppositifolius* (in 5 of the 15 samples), *Chassalia kolly* (in 3 lots) or *Reissantia indica, Macrosphyra longistyla,* and *Brachiaria deflexa* (each dominant in one lot); the rest (4 lots) having a highly mixed undergrowth. Though this part of the forest was particularly well enriched with species from nearby natural forest patches the importance of these species remained still modest, namely 4.2% of all small plants in the small lots.

All above named species are part of the 328 naturally occurring species classified as abundant (category 5), yet they account for only 11.6%. For 64.6% of all local species, less than 20 specimens are known, and for 25.0% only 1–4 specimens could be found despite regular and intensive search. Among the 253 introduced species, only one reached a total population of more than 20 specimens.

Origin of species and successional changes

Identification, particularly of juvenile plants without flowers and fruits, proved to be challenging. Up to 1998 a total of 168 plants of local origin had been identified. By 2004, when the bulk of the land had been acquired, the number increased to 317. Up to 2010 only 7 more species were discovered, and 4 more up to 2016, bringing the total of local species to 328. Another 253 species were introduced from forests from southern Benin (Fig. 2).

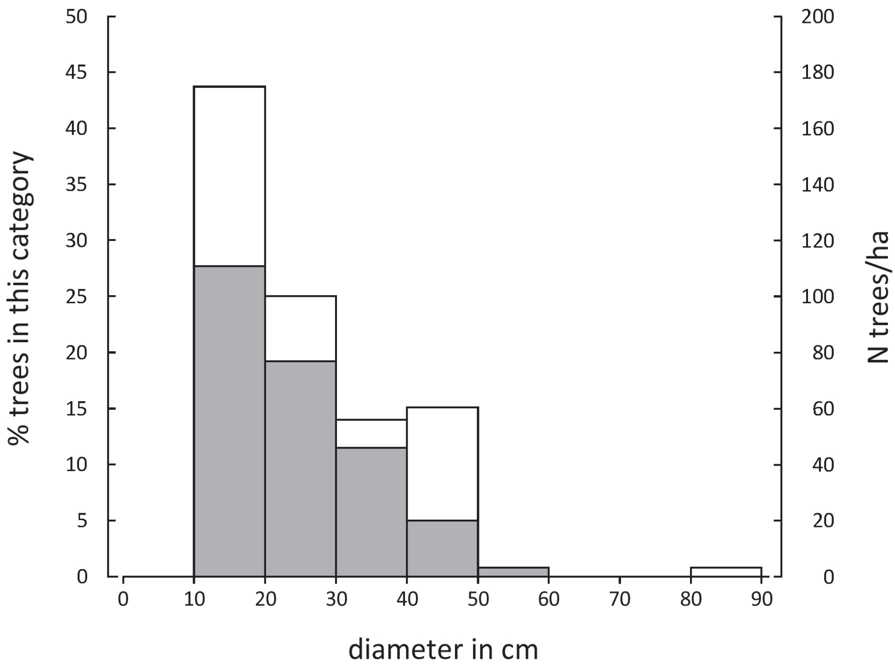

Figure 4. Quantitative assessment. Percentage of trees (N = 119) in classes with diameters of 10 cm differences and estimated numbers per ha. Grey for *Albizia.* Cooun, Drabo Gbo, 2016.

The supplementary file lists 635 plant species, among which four could not yet be identified. Identification or description as a new species will become possible as soon as flowers will be produced. Two have been tentatively attributed to the genus *Monanthotaxis* (Annonaceae).

Among the 631 remaining species, 50 or 7.9% were lost during the last 20 years, 49 of them introduced species. For five of the 10 extra-regional (At, PAL, Pt) and 10 of the savanna (SG, SZ, S) species, loss is attributed to seeds that would not sprout in the forest environment. By contrast, only one out of seven forest (GC) species that had been collected only as seeds failed to produce seedlings.

This leaves 581 species (Table 1) with 244 from Guineo-Congolian forests, among them 17 of Upper Guinean and four of Lower Guinean origin, 113 (81+32) from the three savannah zones, and 224 (80+144) of extra-regional origin. Woody plants, i.e., many climbers, all shrubs and trees, but without parasites and epiphytes, of forest and savanna origin (GC, SG, SZ and S) dominate (72.8%, N = 423) the flora in Drabo, whereas significantly more herbs (70.4%, N = 152) hail from other regions (At, PAL and Pt) (Chi-square = 9139, P<0.001, N = 575).

Since locally occurring rare species were also transplanted to other parts of the forest, the total number of introduction events in the course of the last 20 years was a high 1041, with a maximum of 10 introductions per species with up to 10 individuals from one collection date.

Table 1. Number of species alive and percentage declining (d.) in different ecological zones. Drabo July 2016.

Region	Para. & Epi.		Herbs		Climbers		Shrubs		Trees		Total	
	N	%d.	N	%d.	N	%d.	N	%d.	N	%d.	**N**	**%d**
CG [†]	4	0.0	23	13.0	75	9.3	33	3.0	109	5.5	**244**	**7.0**
SG	0		17	64.7	23	13.0	8	25.0	33	18.2	**81**	**27.2**
SZ and S	0		5	60.0	3	33.3	4	50.0	20	45.0	**32**	**50.0**
At and PAL	0		42	74	17	29.4	6	33	15	27	**80**	**52.5**
Pt	2	50.0	65	80.0	20	65.0	10	70.0	47	42.6	**144**	**64.6**
Total	**6**	**16.7**	**152**	**65.8**	**138**	**21.0**	**61**	**24.6**	**224**	**20.1**	**581** [¥]	**33.0**

[†] including GO (Upper Guinea) 17 spp. and GE (Lower Guinea) 4 spp.
[¥] plus 4 spp. non-identified, 2 of them climbers, 2 shrubs

During the last 20 years, changes in composition were observed. Declines in number of plants and, sometimes, plant vigour were unevenly distributed among growth forms and origins (Table 1). Declines were rare (7.0%) among plants from the GC zone, particularly trees and shrubs. They increased gradually the further away the plants originated from, up to 64.6% among plants of pan-tropical origin. Particularly pan-tropical herbs became rare with 80.0% of all 65 species of this category declining and being confined to the few remaining open spaces and alongside paths.

Change to a more mixed composition of large trees with a larger proportion of evergreen species is reflected in the frequent breaking of large branches of *Albizia* trees during storms, while *Celtis* and *Blighia* spp. resist better and become gradually more important.

The decline in numbers and vigour of particular species in Table 1 indicates the prospective changes in species distribution. Here some examples concerning trees and plants of commercial interest:

A total of 224 tree species are growing on these 14 ha. Among them, 69 are big trees of 10 m height or more. In the Drabo forest under total protection, the number of *Cola gigantea*, which had been largely destroyed in the area, increased steadily. The timber trees *Afzelia africana, Celtis milbraedii*, *Diospyros mespiliformis, Milicia excelsa* and *Triplochiton scleroxylon,* which had all disappeared from Drabo, grew well in the study forest. *Erythrophleum suaveolens* raised from seeds became common and reached 25 m, while *Rhodognaphalon brevicuspe* planted as sticks reached 22 m.

Some formerly rare plants like *Oxyanthus racemosus* and *Pavetta corymbosa*, of which only one plant each could be found in 1995-1996, became common. Similarly, some tree species like *Albizia ferruginea, Borassus aethiopum, Ceiba pentandra, Celtis milbraedii, Parkia biglobosa, Psydrax parviflora, Vepris verdoorniana,* and *Zanthoxylum* *leprieuri* existed in only one lot, but grew well when planted elsewhere. Several trees, which were the last ones in the area and were subsequently felled, provided seeds and sticks that were reared in the nursery and then planted out: *Cynometra megalophylla, Elaeophorbia drupifera, Kigelia africana,* and *Pentaclethra macrophylla*.

Some species from the Guineo-Sudanian transition zone or even further north reach the coast and were found in Drabo, like *Adansonia digitata, Crossopteryx febrifuga, Lawsonia inermis, Parkia biglobosa,* and *Tamarindus indica*, of which only a few big trees survived in the area. *Lophira lanceolata* from the isolated population near Pahou survived only on sandy soil.

The following introduced species came from clines in forests with open water like Pobè and Niaouli; they required irrigation and mulching during the first dry season for establishment: *Barteria nigritana, Cleistopholis patens, Dennettia tripetala, Distemonanthus benthamianus, Entandrophragma angolense, Homalium letestui, Mansonia altissima, Monodora myristica, Piptadeniastrum africanum, Pycnanthus angolensis, Tabernaemontana eglandulosa,* and *Trilepisium madagascariense*.

In the course of reforestation of the last 20 years, yearly herbs decreased or disappeared. They resurged, however, immediately wherever an opening provided sunlight habitat. Thus, *Trema orientalis* trees could not be found anymore, until they suddenly reappeared from dormant seed on MdJ in 2013 in the newly opened up area, hundreds of meters away from the original site. Even in places where *Chromolaena odorata* was not cut, the encroaching forest within 10 years shaded it out completely. *Tithonia diversifolia,* another feared invader, appeared only once in 2002 and disappeared the same year, when shaded out.

Commercialized fruits are produced by the following well-established indigenous trees: *Chrysophyllum albidum*, *Dialium guineense, Irvingia gabonensis,* and *Spondias mombin*. Of particular interest is the introduced *Synsepalum dulcificum*, an endangered plant that has potential for commercialization because of its sugar-free sweet fruits. Tropical crops of closed forests like *Coffea canephora*, *Hevea brasiliensis, Theobroma cacao*, and *Vanilla planifolia* needed irrigation to start growth. By contrast, the exotic fruit trees *Anacardium occidentale*, *Azedirachta indica, Mangifera indica*, and *Psidium guajava* did not last in the closed forest and died within 10-15 years. Similarly, field crops like *Ananas sativus*, *Manihot esculenta,* and *Musa* triploid spp. did not produce any commercial product anymore, but persisted in the closed forest for many years even when shaded.

Among the introduced timber species, *Acacia auriculiformis* and *Cassia siamea* grew well in closed forest, whereas *Leucaena leucocephala* was overgrown by climbers and despite abundant seed-set did not reproduce vigorously. Among the original 1 ha of *Tectona grandis* many trees were cut; but the remainder grew well in a mixed forest. The one clump of *Bambusa vulgaris* remains problematic because it is displacing all other plants in the vicinity.

Many medicinal plants, which grow also in the Drabo forest, like *Acanthus montanus, Mondia whitei, Acridocarpus smeathmanii* and *A. alternifolius,* as well as *Heliotropium indicum* are being commercialized and sold on the "juju" markets, without being cultivated or even locally protected.

Endangered plants

Table 2 lists a total of 73 species from the Red List of Benin (EW, CR, EN or VU only), which could possibly survive in the reconstituted forest, among which 52 species are actually growing in Drabo, i.e., 71.2%. Four more species were planted, but could not survive. Ten species were found in Drabo before introductions from other sites started.

Most threatened (CR) are *Acanthus montanus* which was purchased on the market in Calavi, where material from one location near Porto Novo is sold as medicine; *Barteria nigritana* from Ahozon; *Caloncoba echinata* from a moist site in Niaouli; *Entandrophragma angolense,* which originally had only a few trees in Niaouli; and *Dennettia tripetala* and *Nesogordonia kabingaensis* from Ewè, where they are not protected. *Caesalpinia bonduc* is extinct in the wild (EW), but widely maintained (and also stolen!) in the village for its medicinal roots. A few plants of *Garcinia cola* (EW) also grow in the study forests. Of special interest are *Distemonanthus benthamianus* (EN), which exists in Benin only in one small, though protected site in Pobè, and *Mansonia altissima* (CR) from Ewè, where it is not protected. Both species grow as isolated populations at the eastern edge of their continental distribution, and only few trees exist in Benin.

Thanks to 20 years of careful protection and management, many threatened plants could be established and the species richness of the forest now rivals the one of the forests from where these endangered species come from (Table 2).

Discussion

Biodiversity in general, and of tropical forests in particular, is to be preserved for ethical reasons, for agriculture under the headings of plant protection-biological control (Neuenschwander et al. 2003, van Driesche et al. 2010) and varietal selection (Dansi et al. 2013), and for the preservation of water regimes and mitigation of climate change (Corlett 2014) or other eco-services (Martin 1991, Kuyah et al. 2016, Rowland et al. 2016). In an ideal world, nature protection and agriculture are considered complementary and nature reserves a prudent investment (McNeely and Scherr 2001). Though knowledge and understanding of the interactions with agriculture are increasing rapidly (IAAST 2008, Kuyah et al. 2016, Rowland et al. 2016) destruction of forests continues unabated. For Benin, the legal framework for nature conservation is in place (Republic of Benin 2012), but implementation is often insufficient. The protection and restauration particularly of southern forests has therefore been described as first priority in nature protection (Neuenschwander et al. 2011).

Because of their small sizes, Benin forests would not satisfy the criteria for a key biodiversity area (Secretariat of the Convention on Biological Diversity 2002, Brooks et al. 2006, IUCN 2016, RBG Kew 2016); but they show a particularly interesting history. Generally, forests in West Africa have been advancing since the Ice Ages, 10 000 years BP, though this advance has been marked by recessions and, in the area of

Table 2. Distribution of threatened plant species in southern Benin. Only living woody plants (trees, shrubs, lianas) and species on solid ground (i.e., without plants limited to swamp forests, sandy beaches or rocky outcroppings) are considered. Only VU to EW. Presence = x, origin as in Figure 1.

Family	Species	IUCN[†]	Drabo[¥]	Ewè incl. Kétou	Pobè incl. Sakété	Dangbo	Lama	Niaouli	Ahozon (Pahou)	others	Origin[§]
Acanthaceae	*Acanthus montanus*	CR	x*		x					Bassila, Porto-Novo	GC
Anacardiaceae	*Antrocaryon micraster*	CR[+]			x[a]						GC
Apocynaceae	*Carissa spinarum*	VU	x	(x)	x	x	x	x	x	coast	PAL
Apocynaceae	*Tabernaemontana pachysiphon*	EN	x*		x	x					At
Apocynaceae	*Voacanga africana*	VU	x*	x	x	(x)	(x)	(x)	(x)	north	At
Annonaceae	*Dennettia tripetala*	CR	x*	x			x				GC
Annonaceae	*Monodora myristica*	EN	x*			x		x		Lanzron	GC
Annonaceae	*Xylopia aethiopica*	VU	x*		x	x		(x)	x	north	At
Arecaceae	*Borassus aethiopum*	VU	x	(x)			(x)			across country	SZ
Aristolochiaceae	*Pararistolochia mannii*	EN	**L**	(x)	(x)			(x)	x	Zinvié	GC
Asclepiadaceae	*Mondia whytei*	VU	x	x	x	(x)	x	(x)			SG
Bignoniaceae	*Kigelia africana*	VU	x	(x)	x	(x)	x	(x)	(x)		SG
Burseraceae	*Canarium schweinfurthii*	CR			x[a]						GC
Capparaceae	*Maerua duchesnei*	EN	x*	x	x						SG
Celtidaceae	*Celtis milbraedii*	EN	x*	x		x		x			GC
Clusiaceae	*Garcinia kola*	EW	x*							Ouidah, Porto-Novo	GC
Clusiaceae	*Pentadesma butyracea*	VU	x*							Bassila, Pénésoulou	SG
Combretaceae	*Terminalia superba*	EN	x*		x		x		(x)*	north	GC
Euphorbiaceae	*Discoglypremna caloneura*	VU			x[a]						GC
Euphorbiaceae	*Drypetes aframensis* Hutch.	CR		x[a]							GC
Euphorbiaceae	*Drypetes gilgiana*	CR		x[a]							GC
Flacourtiaceae	*Caloncoba echinata*	CR	x*					x[a]			GO
Flacourtiaceae	*Homalium letestui*	EN	x*		x	x		(x)			GC
Leguminosae-	*Afzelia africana*	EN*	x*	(x)	x	(x)	x	(x)	(x)	north	S
Leguminosae.	*Albizia ferruginea*	VU*	x	x	x	(x)		x	x	Pénéssoulou	GC
Leguminosae.	*Anthonota fragrans*	CR	x*		x					Bonou	GC

Family	Species	IUCN[†]	Drabo [¥]	Ewè incl. Kétou	Pobè incl. Sakété	Dangbo	Lama	Niaouli	Ahozon (Pahou)	others	Origin[§]
Leguminosae.	*Caesalpinia bonduc*	EW	x*	(x)*	x*	(x)*	(x)*	(x)*	(x)*		Pt
Leguminosae.	*Detarium senegalense*	VU			x					north	GC
Leguminosae	*Distemonanthus benthamianus*	EN	x*		x[a]						GC
Leguminosae.	*Hymenostegia afzelii*	EN			x						GC
Leguminosae	*Parkia bicolor*	EN	x*		x	(x)		x		Zinvié	GC
Leguminosae.	*Pentaclethra macrophylla*	VU	x		x	(x)		x			GC
Leguminosae.	*Piptadeniastrum africanum*	VU	x*		x	x		x		Zinvié	GC
Leguminosae	*Tetrapleura tetraptera*	VU	x*		x			x	x	north	GC
Leguminosae	*Amphimas pterocarpoides*	EN			x						GC
Leguminosae	*Pterocarpus erinaceus*	EN	x*		(x)		x			north	S
Malpighiaceae	*Acridocarpus alternifolius.*	EN	x*		x		(x)	(x)	x		GC
Malpighiaceae	*Acridocarpus smeathmanii*	EN	x*	(x)	x						GC
Meliaceae	*Carapa procera*	VU			x			x			GC
Meliaceae	*Entadrophragma angolense*	CR[+]	x*		(x)			x			GC
Meliaceae	*Khaya grandifoliola*	EN[+]	x*				(x)*			Bassila, Zagnanado	GC
Meliaceae	*Khaya senegalensis*	EN[+]	x*	(x)	(x)	(x)	(x)	(x)	(x)	Bassila, Zagnanado	S
Meliaceae	*Trichilia martineaui*	CR						x[a]			GO
Meliaceae	*Turraea heterophylla*	EN	x*		x	x	x	(x)			GO
Moraceae	*Milicia excelsa*	EN[+]	x	x	x	x	x	x	x		GC
Myristicaceae	*Pycnanthus angolensis*	VU	x*		x	x		x	(x)		GC
Orchidaceae	*Angraecum distichum*	EN	x*	x						Djrègbè	GC
Orchidaceae	*Graphorkis lurida*	EN	**L**			x					At
Olacaceae	*Strombosia pustulata*	EN	x*		x	x		x			GC
Oleaceae	*Schrebera arborea*	EN		x						north	GC
Passifloraceae	*Barteria nigritiana*	CR	x*						x		GE
Rubiaceae	*Aidia genipifolia*	EN	x*	x	x	(x)		x	x		GC
Rubiaceae	*Euclinia longiflora*	EN	x*		x	x					GC
Rubiaceae	*Gardenia nitida*	EN	x*	x	x		x				GC
Rubiaceae	*Nauclea diderrichii*	EN[+]	x*		x			x		Lokoli	GC

Family	Species	IUCN[†]	Drabo[¥]	Ewè incl. Kétou	Pobè incl. Sakété	Dangbo	Lama	Niaouli	Ahozon (Pahou)	others	Origin[§]
Rubiaceae	*Psilanthus mannii*	CR	x*		x	x					GC
Rubiaceae	*Tricalysia reflexa*	CR				x[a]					GC
Rutaceae	*Afraegle paniculata*	EN					x			north	At
Rutaceae	*Zanthoxylum gilletii*	EN	**L**		x						GC
Rutaceae	*Zanthoxylum zanthoxyloides*	VU	x	x	(x)	(x)	x	(x)	x		GO
Sapotaceae	*Chysophyllum albidum*	VU	x		x	x		(x)	x		GC
Sapotaceae	*Mimusops andongensis*	EN	x*				x[a]				GC
Sapotaceae	*Synsepalum dulcificum*	EN	x*		(x)					Porto-Novo etc.	GC
Sapotaceae	*Vitellaria paradoxa*	VU	**L**	x						north	S
Simaroubaceae	*Pierreodendron kerstingii*	EN+	x*		x			(x)		Zinvié, north	GO
Sterculiaceae	*Mansonia altissima*	CR	x*	x[a]						Calavi*	GC
Sterculiaceae	*Nesogordonia cabingaensis*	CR	x*	x[a]							GC
Sterculiaceae	*Octolobus spectabilis*	CR		x[a]							GC
Sterculiaceae	*Pterygota macrocarpa*	CR		x[a]							GC
Sterculiaceae	*Triplochiton scleroxylon*	EN+	x	(x)	x	x		x		north	GC
Tiliaceae	*Christiana africana*	EN					x				Pt
Violaceae	*Rinorea dentata*	EN	x*	x	x					Bassila	GC
Violaceae	*Rinorea ilicifolia*	CR		x[a]							GC
Total threatened plant species:		**73**	**52**	**30**	**48**	**28**	**20**	**32**	**18**		

[†] IUCN classification for Benin (Adomou et al. 2011): NT near threatened, VU vulnerable, EN endangered, CR critically endangered, EW extinct in the wild. + also on international Red List. [¥] * introduced; **L** lost; [a] = only known site in Benin where species occurs naturally; (x) new records according to A. Adomou; [§] origin: GC Guineo-Congolian (GO Upper Guinean, GE Lower Guinean), SG Sudano-Guinean, SZ Sudanian, S Sahelian, At Afro-tropical, PAL Paleotropical, Pt Pan-tropical.

the Dahomey Gap, slowed by sea currents and trade winds. Since 2000 years, advances are regular and little influenced by grazing, slash- and-burn agriculture with long fallow-periods, originally with endemic crop like rice and yams, firewood collection for iron-smelting, and home use by low human populations (Giresse 2008). Because close forests develop at annual rainfalls of >1400 mm and existing forests decline if rainfall drops below 1200 mm the area of the Dahomey Gap, including southern Benin, did not reach total forest cover (Giresse 2008). Under the rapid population increase of 10 to 20 times in Benin observed in the 20th century, tree savannah surrounding the rainforest pockets was further degraded (Paradis and Houngnon 1977, Mama et al. 2014) and gave rise to agricultural land under ever shorter fallows. Rainforest vegetation was confined to the often cited, but little studied sacred forests (lately: Agbani 2012, CERF Bénin 2013), some small communal and government forests, as well as riparian forests further north (Natta and van der Maesen 2003).

These forest islands harbour plant species with origins in the biodiversity centres of the Upper or Lower Guinea forest blocks. Today, large contiguous forest areas in West Africa are confined to western Côte d'Ivoire and eastern Liberia for the Upper Guinea block and extreme eastern Nigeria to southern Cameroon for the Lower Guinea block. In most areas designated as evergreen or semi-deciduous humid forest (Figure 1), deforestation has been so pervasive that actual conditions are not that far removed from what is found in the moister parts of the Dahomey Gap. In southern Côte d'Ivoire in the Sikensi block of 20 × 20 km, well within the evergreen forest zone (Figure 1), for instance, forest cover changed from 182 km^2 in 1958 to 149 km^2 in 1990, to 17 km^2 in 2000. Forests of less than 4 ha represent 64% of the forest area (Chatelain et al. 2004). Similarly high deforestation rates with maxima in the 1980s were reported from Nigeria (14.3%) and Côte d'Ivoire (15.6%) (Giresse 2008), demonstrating the difficulty of assigning phyto-ecological zones.

Because of rapid deforestation eight out of 26 commercial timber species of Côte d'Ivoire and Ghana are listed as threatened (Poorter et al. 2004). Some of these species exist in Benin, where their threat status is even higher (Table 2, Adomou et al. 2011; for a more stringent list see Adomou 2005). Table 2 demonstrates the richness of threatened species that grow in Drabo, rivalling the one of well-established larger forest reserves. It must, however, be noted that Benin forests with locally open water, like Pobè, Dangbo, and Niaouli, harbour several additional threatened plants, namely those requiring much higher humidity than found in Drabo; such species were not collected nor evaluated. Several of the listed species, like *Distemonanthus benthamianus* and *Mansonia altissima,* which are moreover at the edge of their continental distributions, occur in only one locality each, which–in the case of *Mansonia*–is unprotected, yet they grow well in Drabo. Despite similar conditions, none of the listed forests has all threatened species. We conclude that, in this highly fragmented landscape, rare species were either destroyed by man or suffered from stochastic loss in isolated habitats where important seed dispersers, like some birds, bats or rats, are no longer present (Fahrig 2003, Klein et al. 2014). In a situation, where creating corridors (Damschen et al. 2006) is no longer possible, introducing rare species into convenient habitats under protection counteracts this loss. Our systematic transfer within the same ecological zone, which did not inflict undue harm in the collection sites, thus saved plants that might otherwise disappear from Benin. In Benin, many of these species are at the edge of their ecological and/or geographical distribution and may therefore be genetically different from those in the centre. Such genetic differences could well give them an advantage to face stress from climate change. Special care to ascertain their survival is therefore justified.

The fact that plants from zones with yearly rainfalls 200 mm above the one in Drabo, as for instance *Baissea zygodioides, Dennettia tripetala, Dracaena phryniodes, Gardenia nitida, Landolphia togolana, Pararistolochia goldieana, Tapura fischeri,* and *Turraea heterophylla* from evergreen forest pockets (Holmgren et al. 2004) survive in Drabo, if watered modestly during the first dry season, is testimony to their great plasticity and adaptability.

At the other extreme, these forests harbour also tree species that must be considered remnants of the savannah into which the advancing forests intruded. These include *Lophira lanceolata,* with its isolated population near Pahou (Paradis et al. 1978) as well as *Adansonia digitata*, *Crossopteryx febrifuga, Parkia biglobosa,* and *Khaya senegalensis*, all characteristic trees of the Sudanian savannah, some with occurrence even in the Sahel savannah. They thereby demonstrate their great adaptability to different climates.

The present long-term observations in Drabo describe the succession towards the climax Guineo-Congolese semi-deciduous forest through natural fallow, enriched with plants from other botanical districts of this zone (Adomou 2011). By planting in clearings similar to natural tree fall and without irrigation, traditional forestry practices used for rehabilitation were employed (Sabogal 2007, Stanturf et al. 2012, Chazdon 2014). By planting *Celtis* spp., the natural succession from leguminous pioneer trees like *Albizia* spp. to Celtidaceae, as observed in Dodja, is being accelerated. In contrast to forests on shallow soil as in IITA-Ibadan, where in some places 40 years were not enough to develop a forest (Neuenschwander et al. 2015), Drabo forests develop on deep soil and, by adding species, reach the semblance of a secondary forest within 20 years.

As the tree canopies close herbs–most hail from outside the region–gradually decline. This concerns particularly grasses, so that only two forest species, *Olyra latifolia* and *Oplismenus hirtellus,* remain. The disappearance of herbs is, however, immediately reversed as soon as free soil appears because of natural tree fall or clearance. Because the Drabo forests are of irregular shape with long edges, many light-demanding species can still survive along the fringes.

Except for bamboo, no plant in Drabo has the potential to become invasive and transform the environment. Even *Chromolaena odorata* and *Imperata cylindrica,* two feared weeds, as well as potential invaders like guava or *Leucaena leucocephala* under the conditions of southern Benin just follow the environmental conditions, but do not transform them (Lincoln et al. 2016). They are easily shaded out and cannot stand up to the pressure from the local vegetation except when situated at the very border of the forest. Moreover, in situations where *C. odorata* becomes an obnoxious climax stage, its biological control is now promising (Prasad et al. 1996, Timbilla 1996, Day et al. 2013).

One cannot step into the same forest twice (paraphrasing Heraclitus); the present text therefore provides only a snapshot. The fact that only a few species were newly detected in the last years indicates that the cumulative list of species has reached a plateau and we can expect only few more discoveries. Since 21 IUCN-listed spp. with good potential for establishment are still lacking (Table 2) some more threatened plants might, however, be introduced in future. Conversely, among the introduced plants, some species are represented only by a few, some even by only one specimen with uncertain survival. Most cultivated plant still present in the forest will disappear altogether, while plants used in traditional medicine will hold steady if sufficiently protected. Due to successional changes, alpha-biodiversity, expressed as the total number of species, will probably decline as seen in other systems (Barlow et al. 2007). It is doubtful that a stable climax will ever be achieved because natural tree fall and edge effects will continue to offer footholds for transient species.

Conclusions

With 585 plant species or about 20% of the Flora of Benin, the Drabo forest have become a sanctuary not only for monkeys but also for rare plants, which themselves again offer the basis for the establishment of rare butterflies and other specialists. The vicinity to big towns and the relatively easy access should allow some eco-touristic development. Since the ownership has been transferred to IITA sustainability should be guaranteed (Neuenschwander et al. 2015).

The present study shows that with relatively modest means, but much patience and perseverance, it is possible to restore, even create de novo, a rainforest. The techniques are available since long time (Dobson et al. 1997, Mansourian et al. 2005). What is needed now is action to create a network of protected forests with exchange of species and local rehabilitation to round up the area of forests and to fill holes created by earlier logging. Most importantly, the local populations have to be involved and see the advantage of such forests or at least not oppose their creation. The 14 ha reserve is not large, but it represents two dozen sacred forests. Contrary to those, it is open to the public. Though it is not "natural" (Willis and Birks 2006) it effectively protects biodiversity in a human-impacted, so-called "gardenized" , landscape.

For the future, the major question remains whether in this densely populated area it will be possible to maintain this sanctuary which has become the best known and fully sampled forest of the entire region, while all other forests are all less well known and probably also less well protected. To assure its sustainability the forest will have to be used for scientific studies and bring benefits to the local population. The present study should thereby serve as a basis.

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References

Adjanohoun EJ, Adjakidjè V, Ahyi MRA, Aké Assi L, Akoègninou A, d'Almeida J, et al. (1989) Contributions aux études ethnobotaniques et floristiques en République Populaire du Bénin. Agence de Coopération Culturelle et Technique, Paris, 895 pp.

Adomou AC (2005) Vegetation patterns and environmental gradients in Benin: Implications for biogeography and conservation. PhD Thesis, Wageningen, Wageningen.

Adomou AC (2011) Phytogeography of Benin. In: Neuenschwander P, Sinsin B, Goergen G (Eds) Protection de la nature en Afrique de l'Ouest: Une Liste Rouge pour le Bénin. Nature conservation in West Africa: Red List for Benin. IITA, Ibadan, Nigeria, 14–20.

Adomou AC, Agbani OP, Sinsin B (2011) Plantes, Plants. In: Neuenschwander P, Sinsin B, Goergen G (Eds) Protection de la nature en Afrique de l'Ouest : Une Liste Rouge pour le Bénin. Nature conservation in West Africa: Red List for Benin. IITA, Ibadan, Nigeria, 21–46.

Adomou AC, Sinsin B, van der Maesen LJG (2006) Phytosociological and chorological approaches to Phytogeography: A study at meso-scale in Benin. Systematics and Geography of Plants 76: 155–178.

Adomou AC, Sinsin B, Akoégninou AA, van der Maesen J (2010) Plant species and ecosystems with high conservation priority in Benin. In: van der Burg X, van der Maesen J, Onanana M (Eds) Systematics of African plants, Royal Botanical Garden, Kew, 429–444.

Agbani OP et al. (2012) Potentiel en diversité biologique des forêts sacrées des Départements de l'Ouémé et du Plateau. Rapport Contrat de Prestation de Service N. 2011/005/ Projet 00076343, 312 pp.

Akoègninou A, van der Burg WJ, van der Maesen LJG [Eds] (2006) Flore analytique du Bénin. Backhuys Publishers, Wageningen, 1034 pp.

APG I (1998) The Angiosperm Phylogeny Group. An ordinal classification for the families of flowering plants. Annals of the Missouri Botanical Garden 85: 531–553. https://doi.org/10.2307/2992015

Barlow J, Gardner TA, Araujo IS, Avilla-Pires TC, Bonaldo AB, Costa JE, Esposito MC et al. (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. PNAS 104: 18555–18560. https://doi.org/10.1073/pnas.0703333104

Booth AH (1958) The Niger, the Volta and the Dahomey Gap as geographic barriers. Evolution 12: 48–62. https://doi.org/10.1111/j.1558-5646.1958.tb02927.x

Brooks TM, Mittermeier RA, de Fonseca GAB, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG et al. (2006) Global biodiversity conservation priorities. Science 313: 58–60. https://doi.org/10.1126/science.1127609

CERF Bénin (2013) Projet d'intégration des forêts sacrées dans le système des aires protégées du Bénin. Répertoire des forêts sacrées dans les départements de l'Ouémé et du Plateau. Centre d'études de recherches et de formation forestières, Bénin, 1–68.

Chatelain C, Dao H, Gautier L, Spichiger R (2004) Forest cover changes in Côte d'Ivoire and Upper Guinea. In: Poorter L, Bongers F, Kouamé FN, Hawthorne WD (Eds) Biodiversity of West African forests: An ecological atlas of woody plants species. CABI Publishing, Cambridge, 15–32. https://doi.org/10.1079/9780851997346.0015

Chazdon RL (2014) Second Growth. The promise of tropical forest regeneration in an age of deforestation. University of Chicago Press, Chicago, London, 449 pp. https://doi.org/10.7208/chicago/9780226118109.001.0001

Corlett RT (2014) Forest fragmentation and climate change. In: Kettle C, Koh LP (Eds) Global forest fragmentation. CAB International, Wallingford, 69–78. https://doi.org/10.1079/9781780642031.0069

Damschen EI, Haddad NM, Orrock JL, Tewksbury JJ, Levey DJ (2006) Corridors increase plant species richness at large scale. Science 313: 1284–1286. https://doi.org/10.1126/science.1130098

Day MD, Bofeng I, Nabo I (2013) Successful biological of *Chromolaena odorata* (Asteraceae) by the gall fly *Cecidochares connexa* (Diptera: Tephritidae) in Papua New Guinea. In: Wu Y, Johnson T, Singh S, Raghu S, Wheeler G, Pratt P, et al. (Eds) Biological Control of Weeds: XIII International Symposium, Waikoloa, Hawaii. [September 2011]

Dobson AP, Bradshaw AD, Baker AJM (1997) Hopes for the future: Restoration ecology and conservation biology. Science 277: 515–522. https://doi.org/10.1126/science.277.5325.515

Dansi A, Orobiyi A, Dansi M, Assogba P, Sanni A, Akpagana K (2013) Sélection de sites pour la conservation *in situ* des ignames sauvages apparentées aux ignames cultivées: cas de *Dioscorea praehensilis* au Bénin. International Journal of Biological and Chemical Sciences 7: 60–74. https://doi.org/10.4314/ijbcs.v7i1.6

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annual Review of Ecology and Evolutionary Systematics 34: 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Hawthorne W, Jongkind C (2006) Woody plants of Western African forests: A guide to the forest trees, shrubs and lianes from Senegal to Ghana. Royal Botanical Garden, Kew, 1023 pp.

Hèdégbètan GC (2011) Etude écologique de l'îlot forestier Bahazoun dans la Vallée du Sitatunga, arrondissement de Kpanroun (Commune d'Abomey-Calavi), Bénin. Licence Professionnelle. GEn/EPAC, Université, Abomey-Calavi.

Holmgren M, Poorter L, Siepel A (2004) What explains the distribution of rare and endemic West African Plants. In: Poorter L, Bongers F, Kouamé FN, Hawthorne WD (Eds) (2004)

Biodiversity of West African forests: An ecological atlas of woody plants species. CABI Publishing, Cambridge, 73–389. https://doi.org/10.1079/9780851997346.0073

IAAST (2008) International assessment of agricultural knowledge, Science and technology for development. Summary approved by governments attending the IAASTD Intergovernmental Plenary in Johannesburg, South Africa. [April 2008]

INSAE (2013) Recensement général de la population et de l'habitat. MDAEP, INSAE, Cotonou, Bénin, 1–8.

IUCN (2016) A global standard for the identification of key biodiversity areas, version 1.0, 1–37.

Juhé-Beaulaton D (2008) Sacred forests and the global challenge of biodiversity conservation: the case of Benin and Togo. Journal for the Study of Religion, Nature and Culture 2: 351–372. https://doi.org/10.1558/jsrnc.v2i3.351

Klein AM, Boreux V, Bauhus J, Chappell MJ, Fischer J, Philpott SM (2014) Forest islands in an agricultural sea. In: Kettle CJ, Koh LP (Eds) Global forest fragmentation. CAB International, Wallingford, 79–95.

Kokou K, Adjossou K, Kokutse AD (2008) Considering sacred and riverside forests in criteria and indicators of forest management in low wood producing countries: The case of Togo. Ecological Indicators 8: 158–169.

Kuyah S, Öborn I, Jonsson M, Dahlin AS, Barrios E, Muthuri C et al. (2016) Trees in agricultural landscapes enhance provision of ecosystem services in Sub-Saharan Africa. International Journal of Biodiversity Science, Ecosystem Services and Management. https://doi.org/10.1080/21513732.2016.1214178

Lincoln TR, Schmidt-Jeffris RA, Del Pozo-Valdivia AI (2016) Management strategies–solutions to grand challenges. American Entomologist 62: 98–107. https://doi.org/10.1093/ae/tmw033

Mama A, Bamba I, Sinsin B, Bogaert J, De Cannière BC (2014) Déforestation, savanisation et développement agricole des paysages de savanes-forêts dans la zone soudano-guinéenne du Bénin. Bois et Forêts des Tropiques 322: 1–11. https://doi.org/10.1079/9781780642031.0079

Mansourian S, Vallauri D, Dudley N [Eds, in cooperation with WWF International] (2005) Forest restoration in landscapes: beyond planting trees. Springer, New York, 437 pp. https://doi.org/10.1007/0-387-29112-1

Martin C (1991) Die Regenwälder Westafrikas. Ökologie, Bedrohung und Schutz. Birkhäuser, Basel, 235 pp.

McNeely JA, Scherr SJ (2001) Common ground, common future: How ecoagriculture can help feed the world and save wild biodiversity. IUCN (Gland); Future Harvest, Washington, D.C., 24 pp.

Nagel P, Sinsin B, Peveling R (2004) Conservation of biodiversity in the relic forest in Benin–an overview. Regio Basiliensis 45: 125–132.

Natta AK, Sinsin B, van der Maesen LJG (2003) A phytosociological study of riparian forests in Benin (West Africa). Belgian Journal of Botany 136: 109–128.

Neuenschwander P, Bown D, Hèdégbètan GC, Adomou A (2015) Protecting rain forest patches in West Africa. Nature Conservation 13: 21–46. https://doi.org/10.3897/natureconservation.13.6539

Neuenschwander P, Langewald J, Borgemeister C, James B (2003) Biological control for increased agricultural productivity, poverty reduction and environmental protection in Africa. In: Neuenschwander P, Borgemeister C, Langewald J (Eds) Biological control in IPM systems in Africa. CABI Publishing, Wallingford, 377–405.

Neuenschwander P, Sinsin B, Goergen G (Eds) (2011) Protection de la nature en Afrique de l'Ouest : Une Liste Rouge pour le Bénin. Nature conservation in West Africa: Red List for Benin. IITA, Ibadan, Nigeria, 1–365.

Paradis G, Houngnon P (1977) La végétation de l'aire classée de la Lama dans la mosaïque forêt-savane du Sud-Bénin (ex Sud-Dahomey). Bulletin di Muséum National d'Histoire Naturelle 503: 169–196.

Paradis G, de Souza S, Houngnon P (1978) Les stations à *Lophira lanceolata* dans la mosaïque forêt-savane du Sud-Bénin (ex Sud-Dahomey). Bulletin Musée Naturelle et Histoire Naturelle, Paris, Botanique 35: 39–58.

Poorter L, Bongers F, Kouamé FN, Hawthorne WD (Eds) (2004) Biodiversity of West African forests: An ecological atlas of woody plants species. CABI Publishing, Cambridge, USA, 1–521. https://doi.org/10.1079/9780851997346.0000

Prasad UK, Muniappan R, Ferrar P, Aeschlimann JP, de Foresta H (Eds) (1996) Distribution, ecology and management of *Chromolaena odorata*. Proceedings of the third Int. Chromolaena Workshop (Abidjan, Côte d'Ivoire), November 1993. University of Guam, Publications 202: 1–213.

RBG Kew (2016) The State of the World's Plants Report. Royal Botanic Gardens, Kew, 1–80.

Republic of Benin (2012) Interministerial Order N°0121/MEHU/MDGLAAT/DC/ SGM/DGFRN/SA Setting the conditions for the sustainable management of sacred forests in the Republic of Benin.

Robbins CB (1978) The Dahomey gap. A reevaluation of its significance as a faunal barrier to West African high forest mammals. Bulletin of the Carnegie Museum of Natural History 6: 168–174.

Rowland D, Ickowitz A, Powell B, Nasi R, Sunderland T (2016) Forest foods and healthy diets: quantifying the contributions. Environmental Conservation 1–13. https://doi.org/10.1017/S0376892916000151

Sabogal C (2007) Site-level restoration strategies for degraded primary forests. In: Rietbergen-McCracken J, Maginnis S, Sarre A (Eds) The forest landscape restoration handbook. Earthscan, London, 83–95.

Secretariat of the Convention on Biological Diversity (2002). Review of the status and trends of, and major threats to, the forest biological diversity. Montreal, SCBD, CBD Technical Series 7: 1–164.

Sinsin B, Kampmann D (Eds) (2010) Atlas de la biodiversité de l'Afrique de l'Ouest, Tome I: Bénin. Cotonou and Frankfurt/Main, 1–726.

Sokpon N, Agbo V (1999) Sacred groves as tools for indigenous forest management in Benin. Annales des Sciences Agronomiques du Bénin 2: 161–175.

Stanturf J, Lamb D, Madsen P (Eds) (2012) Forest landscape restoration integrating natural and social sciences. World Forest. Springer Science and Business, Dordrecht, 1–330.

Timbilla JA (1996) Status of *Chromolaena odorata* biological control using *Pareuchaetes pseudoinsulata*, in Ghana. In: Moran VC, Hoffman JH (Eds) Biological Control of Weeds: Ninth International Symposium, Stellenbosch. [January 1996]

UICN (1996) L'atlas pour la conservation des forêts tropicales d'Afrique. Editions Jean-Pierre de Monza, Paris, 310 pp.

Van Driesche RG, Carruthers RI, Center T, et al. (2010) Classical biological control for the protection of natural ecosystems. Biological Control Supplement 1: 2–33. https://doi.org/10.1016/j.biocontrol.2010.03.003

Willis KJ, Birks HJB (2006) What is natural? The need for a long-term perspective in biodiversity conservation. Science 314: 1261–1265. https://doi.org/10.1126/science.1122667

Supplementary material 1

Table A. Comprehensive list of all plant species of Drabo Gbo, Benin.

Authors: Peter Neuenschwander, Aristide C. Adomou

Data type: species data

Explanation note: Status July 2016. Explanations in Materials and methods.

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REVIEW ARTICLE

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International law and lions (*Panthera leo*): understanding and improving the contribution of wildlife treaties to the conservation and sustainable use of an iconic carnivore

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Abstract

The lion (*Panthera leo*) is featuring ever more prominently on the agendas of international wildlife treaties like the Convention on International Trade in Endangered Species (CITES) and the Convention on the Conservation of Migratory Species of Wild Animals (CMS). Lion range and numbers have declined markedly over the last two decades. In this review we assess the present role of international wildlife treaties with a view to improving their combined contribution to the conservation and sustainable use of lions. Our analysis identifies a substantial body of relevant international wildlife law and, moreover, a significant potential for enhancing the contribution to lion conservation of these global and regional treaties. The time is right to invest in such improvements, and our review renders a range of general and treaty-specific recommendations for doing so, including making full use of the Ramsar Wetlands Convention, World Heritage Convention and transboundary conservation area (TFCA) treaties for lion conservation. The CMS holds particular potential in this regard and our analysis provides strong support for listing the lion in its Appendices.

Keywords

Lion, law, international wildlife law, Convention on Migratory Species (CMS), Convention on International Trade in Endangered Species (CITES), Ramsar Wetlands Convention, World Heritage Convention, Convention on Biological Diversity (CBD)

Introduction

Lion (*Panthera leo*) conservation features prominently on the agendas of international wildlife treaties like the 1973 Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the 1979 Convention on the Conservation of Migratory Species of Wild Animals (CMS or Bonn Convention). Lion range and numbers have declined markedly over the last two decades (Bauer et al. 2016). In this review we assess the present role of international wildlife treaties with a view to improving their combined contribution to the conservation and sustainable use of the lion.

International law and large carnivores

Within the broad arena of the ongoing global biodiversity crisis (Ceballos et al. 2015), large-bodied species are generally more vulnerable than small-bodied species, and their population trends reflect this (Di Marco et al. 2014; Ripple et al. 2014; Ripple et al. 2015). With some exceptions, such as most European large carnivore populations (Chapron et al. 2014), the world's largest carnivores, including lions, are declining, with range contractions and worsening conservation status (Ripple et al. 2014; Bauer et al. 2016). Given the important ecological roles of large carnivores, their demise tends to have negative ecological impacts for other species and ecosystems too (Ripple et al. 2014). Recently, a large number of conservation scientists involved with large carnivore and large herbivore conservation called for 'comprehensive actions to save these iconic wildlife species', appealing to all disciplines involved, and duly noting the role of international wildlife conservation treaties as part of this joint endeavor (Ripple et al. 2016a).

In the overall effort to stem and reverse biodiversity loss, law is a crucial instrument (Chapron et al. 2017), including international wildlife law (Bowman et al. 2010; Trouwborst et al. 2017c). International wildlife law – alternatively referred to as international nature conservation law or international biodiversity law – consists mainly of intergovernmental agreements aimed at conservation of (terrestrial and marine) species, natural areas, ecosystems, and/or biodiversity at large. These have been adopted by states, *inter alia*, with a view to the transboundary movements and occurrence of wildlife populations; the international nature of some of the threats to wildlife; and the notion that biodiversity conservation is considered a 'common concern of mankind', as recorded in the preamble to the 1992 Convention on Biological Diversity (CBD). Effective conservation calls for cross-border approaches and long-term commitments. International law is the pre-eminent mechanism for realizing these, and despite the inherent limitations of international treaties and the various challenges to their effective implementation, many species would have been (even) worse off without international wildlife law (Bowman et al. 2010; Gillespie 2011; Bowman 2016; Trouwborst et al. 2017c).

International wildlife treaties have contributed to biodiversity conservation in many different ways, including through protected areas designated pursuant to international commitments; similarly instigated national legislation regulating wildlife exploitation; enhanced priority accorded to conservation issues on governments' agendas; incorporation of technical guidance adopted by treaty bodies into national action plans and legislation; coordinated collection of data; increased cooperation among and between governmental and non-governmental stakeholders; direct assistance to conservation initiatives through treaties' funding mechanisms; and through many instances where harmful developments were blocked or particular conservation actions taken when governments were confronted with their international obligations in (inter)national court proceedings or compliance mechanisms (Bowman et al. 2010; Gillespie 2011; Trouwborst 2015a; Bowman 2016; Scott 2016; Trouwborst et al. 2017c). There still appears to be significant room for increasing the contribution made by international wildlife law to conservation, not only by enhancing the legal framework itself, but also by maximising the legal instruments currently available (Trouwborst 2015a; Bowman 2016).

Across the globe, large carnivores present a special set of conservation issues from a legal perspective, given *inter alia* their great spatial requirements, elevated human-wildlife conflict potential, and roles as keystone and/or umbrella species (Macdonald et al. 2013; Trouwborst 2015a; Treves et al. 2015). For these reasons, and because of the transboundary nature of many large carnivore populations and some of their threats, international law has a distinct role (Trouwborst 2015a), though this has received little attention in the scholarly literature. Most in-depth research on international law and large carnivores has focused on wolves (*Canis lupus*), brown bears (*Ursus arctos*) and lynx (*Lynx lynx*) in Europe (for a range of examples, see www.clawsandlaws.eu and www.tilburguniversity.edu/iuscarnivoris), with only one general review of the relevance of international wildlife law for the world's 31 largest terrestrial carnivores (Trouwborst 2015a), and one initial analysis focusing on lions in Africa (Watts 2016).

Lions and international law

The lion is archetypal in all of the aforementioned respects. Given its ecological importance as an apex predator, it is a keystone species. It is also an umbrella species, in that lion conservation tends to benefit a range of other species (Caro 2003; Macdonald et al. 2012; Dickman et al. 2015). Lions certainly have large spatial requirements, and coexistence with humans, particularly outside protected areas, is often problematic (Loveridge et al. 2010). There is, moreover, a strong international dimension to lion conservation. Many of the currently remaining lion populations straddle international boundaries (Dickman et al. submitted); close links exist between the conservation and management of lions and international tourism and trophy hunting; the recognition of many natural areas in Africa as sites of international importance under conservation treaties is intimately linked to the presence of lions (Watts 2016); there is an increasing international trade in lion parts (Williams et al. 2015; Williams et al. submitted a;

Williams et al. submitted b); and the worrying conservation status of lions is of international concern to conservationists and to the global public (Macdonald et al. 2016) as one of the most iconic and charismatic species (Macdonald et al. 2015).

Globally, the lion has featured on the IUCN Red List as 'Vulnerable' since 1996. Numbers of wild lions have been steadily decreasing and the global population may be approaching 20,000, with the species persisting in only 8–17% of its historic range (Riggio et al. 2013; Bauer et al. 2016; Dickman et al. submitted). According to the latest Red List assessment, lions remain in 25 sub-Saharan African countries and in a small part of India (Bauer et al. 2016). They have gone extinct in 26 African and Eurasian countries; and are 'possibly extinct' in 7 African countries (Bauer et al. 2016). Dickman et al (submitted) have recently mapped the 60 known remaining populations of lions, and only six of these populations consist of more than 1,000 individuals: Selous-Niassa, Serengeti-Mara, Kavango-Zambezi, Greater Limpopo, Katavi-Ruaha and Kgalagadi (see Figure 1). Just under half of the wild lion estate lies within protected areas, and Lindsey et al. (2017) have demonstrated that even there, in most cases the lions are thought to live well below carrying capacity and at considerable threat from infra-structural inadequacies largely derived from shortage of funds. There is a marked difference between the sharp declines observed in most range states, and the situation in four southern African countries (Botswana, Namibia, South Africa, Zimbabwe) and India, where lion populations have declined only slightly, or are stable or increasing (Bauer et al. 2016). The West African lion subpopulation is listed as 'Critically Endangered' (Henschel et al. 2015). The only remaining population of Asiatic lions (*Panthera leo persica*) is considered 'Endangered' (Breitenmoser et al. 2008), although local human attitudes have been remarkably benign (Venkataraman et al. 2014).

Threats to lions include direct persecution, mainly retaliatory or preventive killing to protect livestock or human life; the depletion of their prey base, mainly due to poaching in connection with an unsustainable bushmeat trade (see also Ripple et al. 2016b; Sandom et al. 2017); habitat loss; and killing fueled by an increasing demand for lion bones and body parts (Bauer et al. 2016; Panthera et al. 2017). The first two of these threats – human-lion conflict and bushmeat poaching – are considered the gravest (Panthera et al. 2017). Trophy hunting can have positive or negative impacts, depending on how well it is regulated (Bauer et al. 2016; Loveridge et al. 2016; Macdonald 2016; Macdonald et al. 2017).

Dickman et al's (submitted) rangewide analysis identifies for each population, and for each country within which lions still occur, the intersection of ecological and infrastructural fragilities. The latter forms a backcloth against which to consider the pattern of international law in those same countries. Against this backcloth, and building on Watts (2016), this review aims to explore the current and potential future utility of international wildlife law for lion conservation. Experience, including our own, indicates that this is best achieved through a multidisciplinary approach (Macdonald and Chapron 2017), whereby legal experts join forces with ecologists and experts from other disciplines with a good understanding of the broader context and the actual

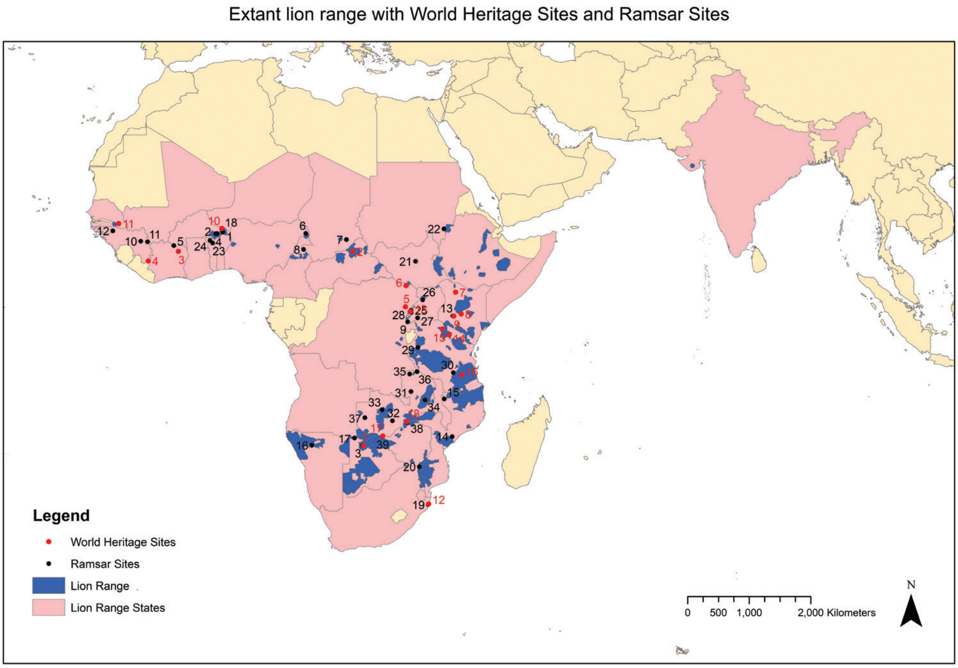

Figure 1. Extant lion range (excluding small fenced reserves), Ramsar-listed sites and World Heritage sites. The numbers indicate the locations of the sites listed in Tables 3 and 4.

conservation needs of species. Such cooperation has, encouragingly, been gathering momentum in recent years (Cliquet et al. 2009; Trouwborst et al. 2015; Epstein et al. 2016; Selier et al. 2016; Treves et al. 2017; Trouwborst et al. 2017a; Chapron et al. 2017; Redpath et al. 2017; Trouwborst et al. 2017c). Our review, performed by legal experts, conservation biologists and social scientists, builds on this momentum.

Though focus is thus on lions, the results of our review are likely to be relevant also for other large carnivore species, particularly in Africa, such as leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*) and hyaenas (*Crocuta crocuta*, *Hyaena hyaena*, *Hyaena brunnea*).

Method

Our analysis is based on standard legal research methodology, involving the selection and interpretation of international legal instruments of relevance to lion conservation (Trouwborst 2015b). For reasons of space, we limit this analysis to international *wildlife* law, although we note the existence of other fields of international law with direct or indirect significance for lion conservation, such as legal instruments dealing with crime, corruption, climate change, or indeed the regulation of pesticides, some of which are used to poison lions (Watts 2016). For each legal instrument, we offer a concise explanation of the most relevant legal obligations (for more exhaustive information on those obligations and general background concerning the treaty regimes involved we refer readers to works such as Bowman et al. (2010) and Gillespie (2011), and the websites of the various treaties). On that basis, we analyze the various legal instruments and obligations within their broader context, incorporating knowledge and insights regarding lions and their conservation needs, and regarding the varying, real-world concerns of the various lion range states and their human populations. We focus on the 33 lion range states identified in the IUCN Red List assessment, including 7 states where lions are considered 'possibly extinct'. We do so in particular with a view to the potential for lion recolonization or reintroduction.

Overview of the international law and policy framework for lion conservation

Binding instruments

Treaties of importance to lion conservation are listed in Table 1. Table 2 and Figure 2 indicate the extent to which the various lion range states are currently bound by eight of these lion-related treaties under international law as contracting parties. The methods employed by the various treaties vary. Some treaties operate on the basis of species lists, with a particular legal regime associated with each list; others involve the listing of sites; yet others do not employ lists. The treaties' geographic scopes also vary.

Five treaties are global. These 'Big 5' of international wildlife law are the 1971 Convention on Wetlands of International Importance Especially as Waterfowl Habitat (Ramsar Convention), the 1972 UNESCO Convention Concerning the Protection of the World Cultural and Natural Heritage (World Heritage Convention or WHC), CITES, CMS and CBD. Lions have been in the spotlight mostly in connection with CITES and, in recent years, the CMS. In May 2016, CITES and CMS jointly hosted an intergovernmental meeting in Entebbe, which was dedicated specifically to African

Table 1. Treaties of relevance to lion conservation. The relevance of each treaty or category of treaties is indicated for African lion subpopulations and Asiatic lion, respectively. N/A = not applicable.

	African lion	Asiatic lion (*P. leo persica*)
Ramsar Convention	Habitat in 39 listed sites	No listed habitat
World Heritage Convention	Habitat in 18 listed sites	No listed habitat
CITES	Listed in Appendix II	Listed in Appendix I
CMS	Not (yet) listed, but covered	Not (yet) listed, but covered
CBD	General relevance	General relevance
African Convention	Listed in Annex, Class B	N/A
Bern Convention	Not listed, but covered	N/A
SADC Protocol	General relevance	N/A
Lusaka Agreement	General relevance	N/A
TFCA treaties	General relevance	N/A

Table 2. Lion range states and their participation in relevant treaties. List of lion range states as provided in the IUCN Red List of Threatened Species 2016 (excluding previous range states in which the species is known to be extinct), indicating their participation in relevant treaties. PE = possibly extinct; X = contracting party; - = not currently a contracting party, but could become one; N/A = not applicable (i.e. the country falls outside of the instrument's geographic scope).

Range state	Ramsar	WHC	CITES	CMS	CBD	African Convention	SADC Protocol	Lusaka Agreement
Angola	-	X	X	X	X	-	-	-
Benin	X	X	X	X	X	-	N/A	-
Botswana	X	X	X	-	X	-	X	-
Burkina Faso	X	X	X	X	X	X	N/A	-
Cameroon	X	X	X	-	X	X	N/A	-
Central African Republic	X	X	X	-	X	X	N/A	-
Chad	X	X	X	X	X	-	N/A	-
Côte d'Ivoire (PE)	X	X	X	X	X	X	N/A	-
Dem. Rep. of Congo	X	X	X	X	X	X	-	-
Ethiopia	-	X	X	X	X	-	N/A	-
Ghana (PE)	X	X	X	X	X	X	N/A	-
Guinea (PE)	X	X	X	X	X	X	N/A	-
Guinea-Bissau (PE)	X	X	X	X	X	-	N/A	-
India	X	X	X	X	X	N/A	N/A	N/A
Kenya	X	X	X	X	X	X	N/A	X
Malawi	X	X	X	-	X	X	X	-
Mali (PE)	X	X	X	X	X	X	N/A	-
Mozambique	X	X	X	X	X	X	X	-
Namibia	X	X	X	-	X	-	X	-
Niger	X	X	X	X	X	X	N/A	-
Nigeria	X	X	X	X	X	X	N/A	-
Rwanda (PE)	X	X	X	X	X	X	N/A	-
Senegal	X	X	X	X	X	X	N/A	-
Somalia	-	-	X	X	X	-	N/A	-
South Africa	X	X	X	X	X	-	X	-
South Sudan	X	X	-	-	X	-	N/A	-
Sudan	X	X	X	-	X	X	N/A	-
Swaziland	X	X	X	X	X	X	-	-
Togo (PE)	X	X	X	X	X	X	N/A	-
Uganda	X	X	X	X	X	X	N/A	X
Un. Rep. of Tanzania	X	X	X	X	X	X	X	X
Zambia	X	X	X	-	X	X	X	X
Zimbabwe	X	X	X	X	X	-	X	-
33	**30**	**32**	**32**	**25**	**33**	**21**	**8**	**4**

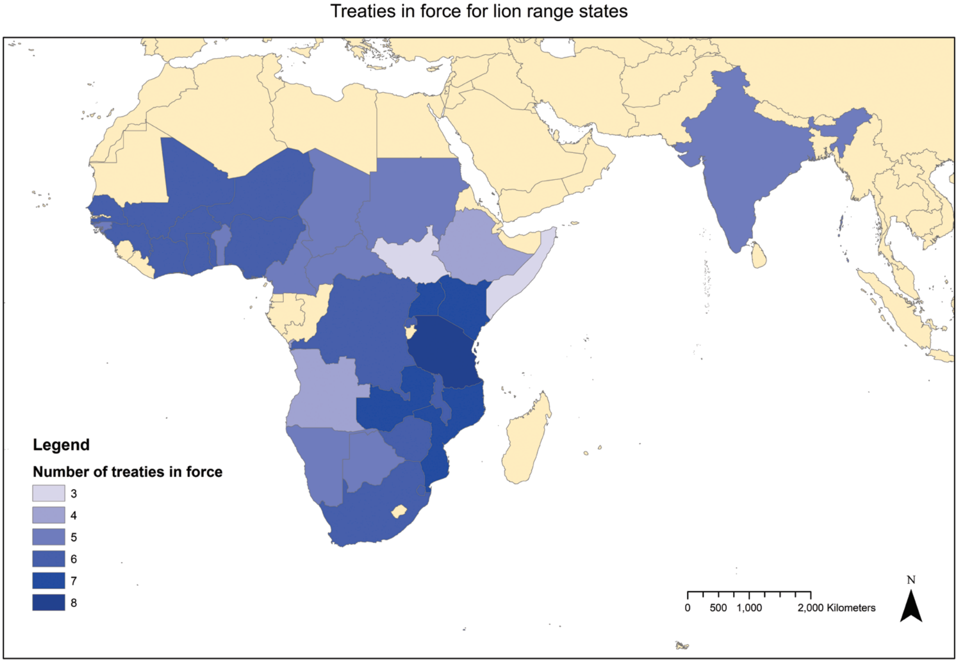

Figure 2. The map shows to how many of the 8 lion-related treaties mentioned in Table 2 each lion range state is a contracting party.

lion conservation and was attended by delegations of 28 of the 33 range states. The five global treaties are analyzed separately below.

Relevant regional treaties are the 1968 African Convention on the Conservation of Nature and Natural Resources (African Convention), the 1994 Agreement on Co-operative Enforcement Operations Directed at Illegal Trade in Wild Fauna and Flora (Lusaka Agreement), the 1999 Protocol (to the 1992 Treaty of the Southern African Development Community) on Wildlife Conservation and Law Enforcement (SADC Protocol), and various treaties establishing transfrontier conservation areas (TFCAs). Curiously, even the 1979 Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) is of potential, albeit more marginal, significance to lion conservation (see below). Pertinent instruments that have not yet entered into force include the 2003 revision of the African Convention and the 2005 Protocol on Environment and Natural Resources Management to the 1999 Treaty for the Establishment of the East African Community (EAC Treaty) – although we note the relevance to lion conservation of some provisions of the EAC Treaty itself.

Below, we provide individual analyses of the most relevant treaties, in particular the Big 5 global conventions, in chronological order of their adoption, followed by selected regional instruments.

Non-binding instruments

The distinction between binding and non-binding instruments is important. Treaties (which can alternatively be titled 'Agreement', 'Convention' or 'Protocol'), when in force, impose obligations on their contracting parties that are binding under public international law. These legal obligations should be distinguished from the host of non-binding instruments called 'Declaration', 'Communiqué', 'Memorandum of Understanding', 'Action Plan', 'Strategy', 'Programme', 'Initiative', and the like. Many of the decisions (Resolutions, Recommendations, etc.) adopted by wildlife treaties' Conferences of the Parties (COPs – their main decision-making bodies in which all parties are represented and which meet periodically) are as such non-binding, although they do have the potential to influence the interpretation of the binding obligations in the treaties themselves.

A pertinent example of a non-binding instrument is the Communiqué adopted by the aforementioned CITES-CMS African lion range state meeting in 2016 (Entebbe Communiqué), and it is worthwhile to reproduce a selection of the statements it contains. The Communiqué records 'the main threats (listed in no particular order) for lions in Africa' to be:

(1) 'Unfavourable policies, practices and political factors (in some countries);
(2) Ineffective lion population management;
(3) Habitat degradation and reduction of prey base;
(4) Human-lion conflict;
(5) Adverse socio-economic factors;
(6) Institutional weakness; and
(7) Increasing trade in lion bones.'

Amongst the recommended measures to counter these threats, the Communiqué issues a call on range states to 'strengthen their legislation on lion conservation' and adopt practices 'ensuring that agricultural activities and mining operations do not impede lion conservation.' Furthermore, and significantly for present purposes, the Entebbe Communiqué recognizes 'the need for transboundary cooperation and management systems in light of the high number of transboundary lion populations.' It also emphasizes the notorious 'lack of resources and capacity,' which has 'impeded the implementation of lion conservation activities on the ground.' Notably, the Communiqué contains the following statement on the controversial issue of lion trophy hunting, wherein the 28 range states that attended the meeting:

'*Highlight* the benefits that trophy hunting, where it is based on scientifically established quotas, taking into account the social position, age and sex of an animal, have, in some countries, contributed to the conservation of lion populations and *highlight* the potentially hampering effects that import bans on trophies could have for currently stable lion populations.'

Generally, the lion range states call upon 'CITES, CMS and IUCN to actively support conservation activities,' *inter alia* through the establishment of a 'mechanism to develop and implement joint lion conservation plans and strategies, capacity-building in lion conservation and management,' and also of a 'fund for specific emergency projects for lion conservation.' In addition, the Communiqué contains several specific considerations regarding CITES and CMS which will be discussed below. Thus, whereas the Entebbe Communiqué is not a legally binding document, it does reflect a consensus amongst 28 range states regarding the threats to lions and the measures to be taken, which can in turn feed into the application of international wildlife treaties to lion conservation.

Of particular significance for present purposes are the two regional Lion Conservation Strategies that were developed in 2006 for West and Central Africa (IUCN 2006a), and Eastern and Southern Africa (IUCN 2006b) respectively. These were prepared by the IUCN SSC Cat Specialist Group, at the instigation of the 13th CITES COP in 2004, and with the support of a range of other stakeholders. The Conservation Strategy for the Lion in West and Central Africa sets out four objectives, together with a range of recommended actions to achieve them: (1) conserve lion habitat in the region; (2) conserve the lion's wild prey base; (3) achieve sustainable human-lion coexistence; and (4) reduce the factors decreasing the viability of lion populations (IUCN 2006a). The overall goal of the Conservation Strategy for the Lion in Eastern and Southern Africa is to 'secure, and where possible, restore sustainable lion populations throughout their present and potential range' within the region, 'recognizing their potential to provide substantial social, cultural, ecological and economic benefits' (IUCN 2006b). Amongst several objectives identified to achieve this, the Strategy recommends the development and implementation of 'harmonious, comprehensive legal and institutional frameworks that provide for the expansion of wildlife-integrated land use, lion conservation and associated socio-economic benefits in current and potential lion range', as well as the alignment of global legal frameworks such as CITES and CMS with the conservation needs of lions in the region (IUCN 2006b). At the request of the 11th CMS COP in 2014, the two regional strategies were reviewed by Bauer et al. (2015). The Entebbe Communiqué adopted by the 2016 CITES-CMS African lion range state meeting affirms that 'all the objectives of the Regional Lion Conservation Strategies … remain valid.' Thus, even if the strategies themselves are not legally binding, we note their close ties with the CITES and CMS legal frameworks in particular, and will revisit their relevance below.

Ramsar Wetlands Convention

In 1971, the Ramsar Convention was adopted in order to 'stem the progressive encroachment on and loss of wetlands' (Preamble). Wetlands are defined in the Convention as 'areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres' (Article 1(1)).

The Ramsar Convention's central feature is a List of Wetlands of International Importance, presently comprising over 2,000 sites spread across 169 countries, whereby it should be noted that many listed wetlands also include dry areas within their boundaries. The Convention's contracting parties 'shall formulate and implement their planning so as to promote the conservation of the wetlands included in the List, and as far as possible the wise use of wetlands in their territory' (Article 3(1)). Notably, the latter half of this obligation applies to *all* wetlands. 'Wise use' of wetlands is understood as 'the maintenance of their ecological character, achieved through the implementation of ecosystem approaches, within the context of sustainable development' (Ramsar COP Resolution IX.1, 2005). Parties to the Ramsar Convention are also required to 'promote the conservation of wetlands … by establishing nature reserves on wetlands, whether they are included in the List or not, and provide adequately for their wardening' (Article 4(1)). They are furthermore expected to cooperate regarding transboundary wetlands and to 'coordinate and support present and future policies and regulations concerning the conservation of wetlands and their flora and fauna' (Article 5).

Adding sites to the Ramsar List is done principally by the contracting parties themselves. Each party must designate at least one site of 'international importance in terms of ecology, botany, zoology, limnology or hydrology' for inclusion in the List (Article 2). For every candidate site, the domestic authority involved completes a 'Ramsar Information Sheet' detailing how the site meets the selection criteria, with the Convention Secretariat verifying that it indeed does so. Parties can coordinate the listing of the respective parts of transboundary wetlands located on their territories, resulting in 'Transboundary Ramsar Sites'. Deletions or boundary restrictions of wetlands on the Ramsar List may be conducted only if an 'urgent national interest' of the contracting party involved so requires, and any associated loss of wetland resources should 'as far as possible' be compensated, for instance by creating additional nature reserves (Articles 2(5) and 4(2)). In order to guide the implementation of the aformentioned legal obligations, a large body of detailed recommendations regarding the conservation and wise use of wetlands has been adopted over the years by the Ramsar COP. For instance, the COP has clarified that any harvesting of wildlife (products) from a Ramsar-listed site should be 'regulated by a management plan developed in close consultation with the stakeholders,' and that the party involved is to 'ensure that the impact of the harvesting will not threaten or alter the ecological character of the site' (Ramsar COP Resolution VII.19, 1999, Annex).

Despite the Convention's initial emphasis on waterbirds, its broad objectives and obligations evidently also cover the conservation of other native wild fauna inhabiting wetlands generally, and wetlands on the List in particular. According to one of the criteria adopted by the COP to guide the selection of wetlands for inclusion in the List 'a wetland should be considered internationally important if it supports vulnerable, endangered, or critically endangered species' (Ramsar COP Resolution VII.11, last amended by Resolution X.20, 2008). Listed wetlands that are under threat can be included in the so-called 'Montreux Record', a register of Ramsar sites 'where changes in ecological character have occurred, are occurring or are likely to occur' (Ramsar COP Recommendation 4.8, 1990).

Ramsar sites of importance to lions

Whereas the Ramsar Convention may not be the first treaty that comes to mind when thinking about lion conservation, lions certainly are amongst the beneficiaries of wetland conservation under the Convention – which currently binds 30 of the 33 lion range states (Table 2). Whereas lions can survive in very arid regions, home ranges normally include one or more sources of water. Besides providing water for the lions to drink, concentrations of prey animals also tend to be above average in riverine or marshy habitat and around waterholes (Valeix et al. 2010). Thus, the conservation and 'wise use' of such wetlands, even if they are small, is important from a lion conservation perspective. Notably, the definition of wetlands used under the Convention lacks a minimum size requirement and includes man-made ones, even 'farm ponds, stock ponds, small tanks' (Ramsar Convention Secretariat 2013), so that pumped water holes in game reserves are clearly covered, and therefore subject to the 'wise use' commitment of Article 3. There is also no minimum size requirement for listing a site as internationally important, with the result that even small or temporary sites may qualify for listing, as may clusters of small sites (Ramsar COP Resolution VII.11, 1999). On the other end of the scale, some African floodplains and other wetland ecosystems are so vast that they include many lion home ranges.

Many sites of significance to lions have been deemed of 'international importance' and included in the Ramsar List. Table 3 renders 39 Ramsar-listed sites which are of actual or potential importance to lions, spread over 19 countries. Their locations are indicated in Figure 1. They cover a total surface area of 368,609 km^2 (an area larger than Germany and almost as large as Zimbabwe). Most of these sites (21) are between 1,000 and 10,000 km^2. Examples are Parc National des Virunga in the DRC, Etosha Pan in Namibia, Kilombero Valley Floodplain in Tanzania (which overlaps with the Selous Game Reserve), Kafue Flats and Luangwa Flood Plains in Zambia, and Mana Pools National Park in Zimbabwe. Eight sites are smaller than 1,000 km^2, but such modest Ramsar sites can still be important for resident lions. Examples include Uganda's Murchison Falls-Albert Delta Wetland System (17,293 ha) and Lake George (15,000 ha), and the Makuleke Wetlands in South Africa (7,757 ha). Ten huge Ramsar sites cover over 10,000 km^2 each, including the Bangweulu Swamps in Zambia, the Zambezi Delta in Mozambique (> 30,000 km^2), and the Okavango Delta System in Botswana (> 55,000 km^2).

In 24 out of 39 cases, the importance of the site for lions, usually alongside other species, is explicit in the official motivation filed by the contracting party for listing the site. (This applies to all sites in Table 3 except Parc National des Virunga; the two 2002 sites in Guinea; Lake Nakuru in Kenya; Estosha Pan in Namibia; Makuleke Wetlands and St Lucia System in South Africa; Sudd in South Sudan; the two sites in Togo; the four sites in Uganda; and Kafue Flats in Zambia.) Further, some of the sites in Table 3 had, or possibly had, lions when designated but (probably) no longer do. Examples are La Foret Classée et Réserve Partielle de Faune Comoé-Léraba in Burkina Faso, the three sites in Guinea, and the two sites in Togo. In such cases, the significance of the

Table 3. Ramsar sites of importance to lion conservation. Whereas most of these sites currently have lions, some sites have been included from which lions have disappeared in the recent past. Map codes indicate the sites' geographic locations as shown in Figure 1. For more detailed information on each site, including the reasons for listing and precise location and delimitation, see the Ramsar Sites Information Service database: http://rsis.ramsar.org/.

Country	Ramsar site	Size (ha)	Since	Map code
Benin	Site Ramsar du Complexe W	895,480	2006	1
	Zone Humide de la Rivière Pendjari	144,774	2007	2
Botswana	Okavango Delta System	5,537,400	1996	3
Burkina Faso	Réserve Totale de Faune d'Arly	134,239	2009	4
	La Foret Classée et Réserve Partielle de Faune Comoé-Léraba	124,500	2009	5
Cameroon	Waza Logone Floodplain	600,000	2006	6
Chad	Plaines d'Inondation des Bahr Aouk et Salamat	4,922,000	2006	7
	Réserve de Faune de Binder-Léré	135,000	2005	8
Democratic Republic of the Congo	Parc National des Virunga	800,000	1996	9
Guinea	Niger-Niandan-Milo	1,046,400	2002	10
	Sankarani-Fié	1,015,200	2002	11
	Gambie-Koulountou	281,400	2005	12
Kenya	Lake Nakuru	18,800	1990	13
Mozambique	Zambezi Delta	3,171,172	2004	14
	Lake Niassa and its Coastal Zone	1,363,700	2011	15
Namibia	Etosha Pan	600,000	1995	16
	Bwabwata-Okavango Ramsar Site	46,964	2013	17
Niger	Parc National du W	220,000	1987	18
South Africa	St Lucia System	155,500	1986	19
	Makuleke Wetlands	7,757	2007	20
South Sudan	Sudd	5,700,000	2006	21
Sudan	Dinder National Park	1,084,600	2005	22
Togo	Parc National de la Keran	163,400	1995	23
	Bassin Versant Oti-Mandouri	425,000	2008	24
Uganda	Lake George	15,000	1988	25
	Murchison Falls-Albert Delta Wetland System	17,293	2006	26
	Lake Mburo-Nakivali Wetland System	26,834	2006	27
	Rwenzori Mountains Ramsar Site	99,500	2008	28
United Republic of Tanzania	Malagarasi-Muyovozi Wetlands	3,250,000	2000	29
	Kilombero Valley Floodplain	796,735	2002	30
Zambia	Bangweulu Swamps	1,100,000	1991	31
	Kafue Flats	600,500	1991	32
	Busanga Swamps	200,000	2007	33
	Luangwa Flood Plains	250,000	2007	34
	Mweru wa Ntipa	490,000	2007	35
	Tanganyika	230,000	2007	36
	Zambezi Floodplains	900,000	2007	37
Zimbabwe	Mana Pools National Park	220,034	2013	38
	Victoria Falls National Park	1,750	2013	39

Ramsar designation could, and should, be to safeguard the habitat and prey base of lions (Sandom et al. 2017) so that recolonization or reintroduction remains a future option. The same is true of some Ramsar sites in range states where lions are presently considered extinct. An example is Odzala Kokoua in Congo, which was included in the Ramsar List in 2012 on the basis of documentation mentioning lions as still present within the site. An instance where lions were reintroduced into an area that was designated a Ramsar site when lions were absent is the St Lucia System in South Africa (designated in 1986, lions reintroduced in 2013). One site from Table 3 is listed on the Montreux Record, namely Lake George in Uganda.

Using the Ramsar Convention for lion conservation

Protected areas are crucial to lion conservation. According to Lindsey et al. (2017), *given adequate management*, Africa's protected areas could theoretically support over 80,000 lions – up to four times the total wild lion population remaining in Africa today. Compliance by contracting parties with their legal obligations under the Ramsar Convention in respect of the sites in Table 3 will thus clearly benefit lion conservation. In practical terms, the Ramsar status of a site and the accompanying international obligations are likely to be distinct factors influencing range state authorities, including courts, when deciding whether to authorize certain development projects or other human uses within the site (Gardner et al. 2009). Allowing unsustainable levels of lion killing or bushmeat poaching would certainly be at odds with parties' obligations regarding conservation and 'wise use', especially so for sites where lions were part of the reasons for Ramsar-listing. The inclusion of a site on the Ramsar List thus provides a layer of protection, in addition to any designations of the area under national legislation or, indeed, other international instruments.

Added to this is a range of associated benefits, such as the development of (more rigorous) site management plans following listing and the attraction of additional funding. The latter can be pursued *inter alia* through the Small Grants Fund established in 1990 to aid developing countries in achieving wetland conservation and the sustainable development of local communities depending on wetlands. To illustrate, actions funded under this scheme have included the development of management plans and of measures to control wildlife harvesting, for instance patrol vehicles. Gardner et al. (2009) found that Ramsar-listing for 26 African sites has been instrumental in providing increased support for protection and management of the sites, scientific studies, funding opportunities, tourism, and poverty alleviation. Lastly, multinational corporations, while not legally bound by the terms of the Convention (only states can be contracting parties), can also self-impose commitments towards the conservation of Ramsar sites as part of their corporate social responsibility policies. For instance, in 2014 HSBC (one of the world's largest banking and financial services holdings) adopted a policy in which it instructs all its businesses to 'make appropriate enquiries and not knowingly provide financial services directly supporting projects which threaten the special characteristics of UNESCO World Heritage Sites or Ramsar Wetlands' (HSBC 2014). The policy notes that the risks of such irresponsible investments are 'particularly high in the forestry, agriculture, mining, energy, property and infrastructure development sectors' (HSBC 2014).

From a lion conservation perspective it seems worthwhile, therefore, to make the most of the Ramsar Convention as it currently applies to lion habitat, and to promote the inclusion of further wetlands of importance to lions in the Ramsar List. Examples of such candidate sites for future Ramsar-listing include Usangu Flats and other wetland areas within Ruaha National Park in southern Tanzania, the importance of which is discussed below.

World Heritage Convention

Broadly similar considerations apply with regard to the other global site-based treaty, the UNESCO World Heritage Convention (WHC), the purpose of which is to conserve both cultural and natural heritage. Many ecologically important areas in Africa qualify as 'natural heritage' as understood in the Convention (Article 2), whereby 'outstanding universal value' from an aesthetic, scientific or conservation point of view is the common denominator. A selection of these sites has hitherto been included on the World Heritage List. Unlike the Ramsar Convention, decisions regarding the inclusion of sites are not made by individual states, but by the World Heritage Committee, the Convention's central decision-making body with a rotating membership of 21 states parties (Article 11). The first step to be made by a party is to draw up a 'Tentative List' of outstanding sites on its territory. From this inventory, it may then proceed to nominate individual sites formally, whereby it is for the nominating party to demonstrate the site's outstanding universal value. The nomination is evaluated by the IUCN in an advisory capacity, after which the World Heritage Committee takes the final decision whether to inscribe the site on the World Heritage List. Whereas most sites are within a single country, the List also includes a number of transboundary sites.

Each party 'will do all it can' to fulfill its 'duty of ensuring the identification, protection, conservation, presentation and transmission to future generations' of the natural heritage on its territory, 'to the utmost of its own resources' and, where appropriate, 'with any international assistance and co-operation' (Article 4). It is recalled in this regard that 'natural heritage' includes, but is not limited to, sites on the World Heritage List. Furthermore, to warrant that 'effective and active measures' are taken for the protection of the sites involved, the WHC requires that each contracting party 'shall endeavor, in so far as possible, and as appropriate for each country,' to 'take the appropriate legal, scientific, technical, administrative and financial measures necessary for the identification, protection, conservation, presentation and rehabilitation of this heritage,' and to 'integrate the protection of that heritage into comprehensive planning programmes' (Article 5). The Operational Guidelines of the WHC instruct parties to provide for a buffer zone when this is necessary for a site's proper conservation (World Heritage Committee 2016). A World Heritage Fund (Article 15) is administered by the Committee to provide targeted assistance for the conservation of specific sites. The Committee also administers the List of World Heritage in Danger – the WHC equivalent of the Ramsar Convention's Montreux Record – which flags sites that are 'threatened by serious and specific dangers' (Article 11(4)). Based on a broad mandate to oversee the implementation of the WHC, the World Heritage Committee regularly adopts decisions urging particular parties to adopt particular site-specific measures. As a last resort, the Committee may delete a site from the World Heritage List altogether.

World Heritage sites of importance to lions

Lions in various parts of Africa profit from the WHC, in a manner broadly similar to the Ramsar Convention. All of the 33 lion range states except Somalia are currently amongst the 193 contracting parties to the WHC (Table 2). Table 4 portrays 18 sites, in 15 range states, which are included in the World Heritage List and which are of actual or potential importance to lion conservation. Their locations are indicated in Figure 1. For many of these sites, lions are expressly mentioned in the listing justification. In the aggregate, the 18 sites cover a surface area of 174,630 km^2 (209,453 km^2 when including buffer zones). As with Ramsar, most sites (8 out of 18) are between 1,000 and 10,000 km^2. These include Virunga and Garamba National Parks in the DRC, Niokolo-Koba National Park in Senegal, Mana Pools/Sapi/Chewore in Zimbabwe, and the Ngorongoro Conservation Area in Tanzania – an area which has one of the highest densities of lions in the world. Four sites are smaller than 1,000 km^2, including the transboundary Mount Nimba Strict Nature Reserve in Côte d'Ivoire and Guinea, and the Kenya Lake System in the Great Rift Valley. Six of the listed sites are over 10,000 km^2 in size, including the Okavango Delta in Botswana, Serengeti National Park and Selous Game Reserve in Tanzania, and the recently designated trilateral W-Arly-Pendjari Complex in Niger, Benin and Burkina Faso – the latter site hosting the sole remaining lion population of significance in West Africa. Lions are (probably) gone from some of the sites listed in Table 4, such as Comoé National Park and Mount Nimba, but WHC protection can help keep options open for future reintroduction or recolonization by preserving lion habitat and prey. Seven of the sites in Table 4 are presently included in the List of World Heritage in Danger, while two further sites were temporarily Danger-listed in the past. It will be noted that various of the World Heritage sites in Table 4 partially or completely overlap with Ramsar sites, for instance Virunga National Park (DRC), the W-Arly-Pendjari Complex, the Okavango Delta (Botswana) and Mana Pools National Park (Zimbabwe). As for possible future World Heritage listings, Table 5 renders 26 sites which feature in the Tentative Lists of 14 range states, the successful nomination of which would appear beneficial to lions. Regarding Asiatic lions, the Gir Wildlife Sanctuary was nominated by India in the past, but the World Heritage Committee decided in 1992 that the site did not meet the strict criteria for inclusion in the List.

Table 4. Sites on the World Heritage List of importance to lion conservation. Whereas most of these sites currently have lions, some sites have been included from which lions have disappeared in the recent past. Map codes indicate the sites' geographic locations as shown in Figure 1. For more detailed information on each site, including the reasons for listing and precise location and delimitation, see http://whc.unesco.org/en/list/. B.z. = buffer zone; In danger = listing on List of World Heritage in Danger.

Country	World Heritage site	Size (ha)	Since	In danger	Map code
Botswana	Okavango Delta	2,023,590 + b.z. 2,286,630	2014	-	1
Central African Republic	Manovo-Gounda St Floris National Park	1,740,000	1988	1997-present	2
Côte d'Ivoire	Comoé National Park	1,150,000	1983	2003-present	3
Côte d'Ivoire & Guinea	Mount Nimba Strict Nature Reserve	18,000	1981	1992-present	4
Democratic Republic of the Congo	Virunga National Park	800,000	1979	1994-present	5
	Garamba National Park	500,000	1980	1984-1992 1996-present	6
Kenya	Lake Turkana National Parks	161,485	1997	-	7
	Mount Kenya National Park/ Natural Forest	202,334 + b.z. 69,339	1997	-	8
	Kenya Lake System in the Great Rift Valley	32,034 + b.z. 3,581	2011	-	9
Niger, Benin & Burkina Faso	W-Arly-Pendjari Complex	1,494,831 + b.z. 1,101,221	1996/ 2017	-	10
Senegal	Niokolo-Koba National Park	913,000	1981	2007-present	11
South Africa	iSimangaliso Wetland Park	239,566	1999	-	12
Uganda	Rwenzori National Park	99,600	1994	1999-2004	13
United Republic of Tanzania	Ngorongoro Conservation Area	809,440	1979	1984-1989	14
	Serengeti National Park	1,476,300	1981	-	15
	Selous Game Reserve	5,120,000 + b.z. 21,492	1982	2014-present	16
Zambia & Zimbabwe	Mosi-oa-Tunya / Victoria Falls	6,860	1989	-	17
Zimbabwe	Mana Pools National Park, Sapi and Chewore Safari Areas	676,600	1984	-	18

Using the WHC for lion conservation

In parallel to the discussion above regarding the Ramsar Convention, compliance by lion range states with their obligations under the WHC appears to render distinct advantages from a lion conservation perspective. For World Heritage sites with lions these obligations would include the prevention or mitigation of human-lion conflict and of prey depletion. Designation as World Heritage entails significant prestige, owing in part to the strict selection criteria and external designation process. This prestigious status puts real weight in the scales of governmental decision-making regarding activities potentially affecting listed sites. Likewise, the possibility of a site being stripped of its World Heritage designation is a significant incentive for states to comply with their commitments under

Table 5. Sites of importance to lion conservation on range states' tentative World Heritage lists. Whereas most of these sites currently have lions, some sites have been included from which lions have disappeared in the recent past. For more detailed information on each site, see http://whc.unesco.org/en/tentativelists/.

Country	Site on Tentative List	Since
Botswana	Chobe Linyanti System	2010
	Makgadikgadi Pans Landscape	2010
	Central Kalahari Game Reserve	2010
Cameroon	Parc National de Waza	2006
Chad	Parc National de Zakouma	2005
Ethiopia	Bale Mountains National Park	2008
Ghana	Mole National Park	2000
Kenya	Lake Nakuru National Park	1999
	Aberdare Mountains	2010
	The African Great Rift Valley – Hell's Gate National Park	2010
	The African Great Rift Valley – The Maasai Mara	2010
	The Great Rift Valley – The Kenya Lakes System	2010
	The Meru Conservation Area	2010
	Tsavo Parks and Chyulu Hills Complex	2010
Malawi	Nyika National Park	2000
	Vwaza Marsh Wildlife Reserve	2011
Mali	La Boucle du Baoulé	1999
	La Réserve de Biodiversité du Parc du Bafing Makana	2016
Namibia	Brandberg National Monument Area	2002
	Etosha Pan	2016
	Okavango Delta	2016
Niger	Zone Giraphe	2006
Nigeria	Gashaki-Gumpti National Park	1995
Sudan	Dinder National Park	2004
Togo	Parc National de la Kéran et la Réserve de Faune Oti-Mandouri	2002
United Republic of Tanzania	Eastern Arc Mountains Forests of Tanzania	2006

the Convention. This possibility is a 'stick' at the disposal of the World Heritage Committee that the Ramsar Convention lacks. The Committee is also in a position to require that measures for a site's protection and management be in place *before* it is inscribed on the List – which again is a significant advantage over the Ramsar Convention's procedure.

Overall, the WHC adds a substantial layer of legal protection and a range of associated benefits in respect of listed sites. For an accessible overview and discussion of the benefits of the WHC for wildlife conservation generally we refer to Bertzky (2014). Here, we provide a few examples from the past to illustrate the different ways in which the WHC can serve lion conservation. In 1984, the World Heritage Committee decided to include the Ngorongoro Conservation Area in the List of World Heritage in Danger, after a lack of management had led to the site's overall deterioration. In subsequent years, thanks in part to the Committee's active engagement and technical cooperation projects, the situation improved and the site was removed again from the Danger List. More recently, the Tanzanian government reversed its plan to upgrade a road bisecting the Serengeti National Park into a 'Serengeti Super Highway', under pressure from the World Heritage Committee and, in particular, from two rulings of the East African Court of Justice in 2014 and 2015. In the latter, the Court determined that upgrading the road would be contrary to Tanzania's environmental obligations under the EAC Treaty, while leaning heavily on the Serengeti's World Heritage status in reaching this verdict (Reference No. 9 of 2010, 20 June 2014; Appeal No. 3 of 2014, 29 July 2015). A final illustration concerns the role of multinational corporations. Whereas these are not bound by the WHC as such, an increasing number of them have undertaken 'no-go' commitments regarding sites on the World Heritage List. Besides the aforementioned HSBC policy, the International Council of Mining and Metals and oil companies like Shell, SOCO, Total and Tullow Oil have undertaken not to explore in or extract from World Heritage sites (http://whc.unesco.org/en/extractive-industries). That recurrent threats of mineral extraction activities in sites like Kenya's Lake Turkana and the DRC's Virunga National Park have to date been kept at bay has been due in large part to these sites' World Heritage status.

Evidently, the listing of a site on the World Heritage List or the Danger List does not as such guarantee conservation success. For example, despite its status as a World Heritage site since 1981 and its Danger-listing in 2007, Senegal's Niokolo-Koba National Park has experienced calamitous declines in prey populations, and concomitant declines in lion numbers (Henschel et al. 2014). The IUCN estimates the lion population has declined by 92%, from over 200 animals to only 16, between 1993 and 2014 (Bauer et al. 2016). Even so, the situation might have been even worse without the site's World Heritage status, and that status would also appear to increase the possibilities for promoting recovery.

On the basis of the foregoing, on the whole it appears sensible to seek out and use the existing opportunities for making the most of the WHC for lions occurring in extant World Heritage sites, and to actively work towards the future listing of tentative and other potential heritage sites of importance to lions. One significant candidate site, despite not being tentatively listed yet, is Ruaha National Park in southern Tanzania. This largest National Park in East Africa is the core protected area for the world's second largest lion population (Dickman et al. submitted; Riggio et al. 2012), and has very high levels of anthropogenic lion killing on its borders (Abade et al. 2014). However, it has long been over-looked in terms of its international importance, despite being highlighted as a Key Landscape for Conservation (KLC) by the European Commission (2016), and as a priority area in international and national lion action plans (IUCN 2006b; TAWIRI 2007). World Heritage listing could be a welcome improvement of its global recognition and protected status.

Lions as 'World Heritage species'

As an epilogue to this section, we draw attention to intermittent calls for the intergovernmental recognition of certain species of outstanding universal value as 'World Heritage species' (Wold 2008; Wrangham et al. 2008; Hance 2016). Whereas, conceptually, a good case can be made that lions – alongside other candidates like elephants, tigers and great apes – are species of 'outstanding universal value' and should be considered part of the world's common heritage, the WHC currently only provides a legal basis for declaring *sites*, not *species*, as World Heritage. Providing such a legal basis would require amendment of the WHC or the conclusion of a separate legal instrument dedicated to World Heritage Species (Wold 2008; see also Arthur 2014).

Convention on International Trade in Endangered Species (CITES)

With the sole remaining exception of newly independent South Sudan, all lion range states are currently parties to CITES (Table 2). The purpose of the Convention is to prevent species from being over-exploited through international trade by requiring its parties to impose restrictions on the international trade of plants and animals (and the parts and derivatives thereof) which belong to species, subspecies or populations listed on one of the CITES appendices. Restrictions are implemented through a system of permits, and the level of restriction corresponds with the level of danger faced by the species: Appendix I species are threatened with extinction and are therefore subject to a ban on international commercial trade (Article III); while trade in Appendix II species – which are not yet threatened with extinction, but may become so in the absence of trade regulation – is essentially permissible, provided that it is not detrimental to the species' survival (Article IV). Several types of specimens are exempted from CITES' usual restrictions, including, under certain (complex) conditions, 'personal or household effects', such as hunting trophies (Article VII(3); Res. Conf. 13.7 (Rev. CoP17)). Captive-bred animals belonging to Appendix I species are treated as if included in Appendix II (Article VII(4)). More tailored restrictions can be imposed through annotations to a species' listing, which define the scope of its inclusion in one of the appendices (Res. Conf. 11.21 (Rev. CoP17)).

While CITES' legal text is silent on the use of quotas to limit trade in listed species, the establishment of, and adherence to, quotas is an effective means of satisfying the Convention's requirement that trade not be detrimental. Quotas can be established by the COP through either annotation (for instance, the cheetah's listing is accompanied by an annotation which expresses annual export quotas for live specimens and hunting trophies from Botswana, Namibia and Zimbabwe) or resolution (for instance, Res. Conf. 10.14 (Rev. CoP16) recommends quotas for the harvest of leopards for export from 12 range states). More commonly, however, parties establish quotas unilaterally at the national level. Parties which fail to comply with their CITES commitments risk being penalized with trade suspensions (Res. Conf. 14.3), and, as also tends to be the case with other conservation treaties, parties to CITES are allowed to adopt domestic measures that are stricter than those required by the Convention (Article XIV(1)).

CITES, lion hunting trophies, and trade in lion bones and body parts

Given the international movement of hunting trophies and the increasing demand for lion bone and body parts, CITES clearly has a key role to play in protecting lions against overexploitation. That said, the divergence between lion population trends in certain southern African countries and those in the remainder of Africa, combined with the polarized nature of the trophy hunting debate (Bauer et al. 2015), have made it challenging for CITES' parties to agree on the extent to which trade should be permitted under the Convention. Since 1977, the Asiatic lion has been listed on Appendix I and the African lion populations on Appendix II. In addition, three range states (Guinea, Guinea-Bissau and Somalia) are currently subject to trade suspensions targeting all commercial trade in CITES-listed species – including lions (http://cites.org/eng/resources/ref/suspend.php). A growing number of parties, including Australia, the European Union and the United States, are imposing stricter domestic measures in respect of lions, ranging from more onerous import requirements than are prescribed by CITES to complete prohibitions on the import of hunting trophies from wild and/or captive-bred animals (CoP17 Prop.4; US Fish and Wildlife Service 2015; see also Macdonald 2016). Declared lion item exports for the period 2005–2014 numbered 29,214 items, of which 11,164 were wild sourced (although the definition of wild-sourced is ill-defined, creating some uncertainty); roughly two-thirds of these items were exported from South Africa – which has an active captive lion breeding industry (Williams et al. 2015) – with other exporters including Botswana, Ethiopia, Mozambique, Namibia, Tanzania, Zambia, and Zimbabwe (CoP17 Prop.4). Of these states, only three (Ethiopia, Mozambique and Zambia) appear to have notified the CITES Secretariat that they use national quotas as a means of ensuring the sustainability of lion exports (Table 6).

Proposals to up-list the African lion to Appendix I were submitted by Kenya in 2004 (CoP13 Prop.6) and by nine countries from West and Central Africa – all of which are either currently part of, or have historically belonged to, the lion's range – in 2016 (CoP17 Prop.4). In the Entebbe Communiqué, which preceded the 17th CITES COP in the same year, range states highlighted the importance of considering the latter proposal against the relevant CITES listing criteria. They further recognized that:

'Lion Range States have different views on the inclusion of all African populations of *Panthera leo* in Appendix I, with some arguing that the populations in West and Central Africa are fragmented and highly threatened; and others arguing that the species does not meet the listing criteria and is threatened by factors other than those CITES can address.'

Following the subsequent negotiations during the 17th CITES COP, the African lion was ultimately retained on Appendix II. A new annotation was, however, added to the Appendix II listing, which sets a zero annual export quota for 'specimens of bones, bone pieces, claws, skeletons, skulls and teeth removed from the wild and traded for commercial purposes', but allows the trade of specimens of bones etc. derived from South Africa's captive breeding operations, provided that national export quotas are es-

Table 6. Unilaterally-set quotas for the export of *Panthera leo* specimens. Data from http://www.cites.org/eng/resources/quotas/index.php.

Range State	Year	Quantity	Type of specimen
Ethiopia	2017	10	trophies
	2016	10	
	2015	10	
	2014	10	
	2013	5	
	2012	10	
	2011	10	
	2009	20	
	2008	20	
	2007	20	
		80	skins
	2006	20	trophies
		80	skins
	2005	20	trophies
		80	skins (confiscated)
	2004	20	trophies
		80	skins
	2003	12	trophies
	2002	30	trophies
	2001	15	live & trophies
	2000	10	live & trophies
Mozambique	2017	54	trophies, wild taken
	2016	54	
	2015	60	
	2014	53	wild taken
	2013	50	
	2012	50	
Zambia	2017	24	wild taken
	2016	24	

tablished and communicated to the CITES Secretariat. South Africa has set an export quota at 800 lion skeletons (Department of Environmental Affairs 2017). The concern remains that allowing any trade of lion parts is potentially problematic from an enforcement point of view and has the potential to stimulate demand, and thus poaching (Williams et al. 2015). In this regard, the COP retains the discretion to amend this annotation in the future so as to provide for a more uniform treatment of lion parts regardless of their origin, or to include further conditions in respect of permissible trade. It could, for instance, be required that the proceeds of trade be used for lion conservation and development initiatives benefiting rural communities in lion range, thus assisting in the mitigation of human-lion conflict. A precedent for the latter approach was set by the annotations restricting trade in elephant ivory.

In addition to its inclusion of a new annotation on the international trade of lion parts, the 17th CITES COP adopted a series of decisions on the African lion (discussed below), as well as a resolution on trade in hunting trophies (Res. Conf. 17.9), which seeks to strike a balance between recognizing the potential benefits of trophy hunting and preventing this practice from occurring at unsustainable levels. In the resolution, the COP recognizes that 'well-managed and sustainable trophy hunting is consistent with and contributes to species conservation, as it provides both livelihood opportunities for rural communities and incentives for habitat conservation, and generates benefits which can be invested for conservation purposes.' At the same time, the COP agrees that (even when treated as a personal or household effect) the export of hunting trophies should generally be conditional upon the issuance of an export permit, and thus the making of a non-detriment finding. The resolution further provides guidance on the sustainable management of trophy hunting, and recommends, *inter alia*, that parties 'consider the contribution of hunting to a species' conservation and socio-economic benefits, and its role in providing incentives for people to conserve wildlife, when considering stricter domestic measures and making decisions relating to the import of hunting trophies'.

Under the current Appendix II listing, African states are limited in the types of lion specimens that they may export for commercial purposes, and a party which allows trade to occur at levels that are detrimental to the species' survival will be in breach of its CITES commitments. Were all African lion populations ever to be moved to Appendix I in the future, the types of trade allowed by the Convention would become even more constrained. However, barring additional restrictions through annotations or stricter domestic measures, trade in captive-bred lions could continue for commercial purposes. Moreover, as illustrated by CITES' approach to cheetahs and leopards – both of which appear on Appendix I – the continued export of hunting trophies would also be possible, provided that this is not detrimental to the survival of the population involved. An alternative approach could be to retain some countries' lion populations on Appendix II, while shifting the remainder to Appendix I. The COP has already allowed such 'split-listing' for two other members of Africa's 'Big 5' – the African elephant (*Loxodonta africana*) and the white rhinoceros (*Ceratotherium simum*) – in order to accommodate the trade of animals from certain well-managed populations of these species in southern Africa (see e.g. Lewis 2009). The COP has also, however, cautioned that split-listing should generally be avoided 'in view of the enforcement problems it creates' (Res. Conf. 9.24 (Rev. CoP17)).

The CITES Animals Committee is tasked with conducting 'periodic reviews' of the species appearing in the Convention's appendices, with the purpose of advising the COP on whether particular species are appropriately listed, based on current biological and trade information in light of the applicable listing criteria (Res. Conf. 14.8 (Rev. CoP17)). *Panthera leo* was included in this process in 2011 and, in 2014, a draft review (suggesting that the African lion's Appendix II listing remained appropriate (AC27 Doc. 24.3.3)) was presented to the Committee, which considered it necessary to incorporate information from the lion's 2015 IUCN Red List Assessment before finalizing the document. The review had not been finalized by the 17th COP in 2016, at which stage the need for its completion fell away as a result of the COP making a decision on the lion's proposed up-listing (CoP17 Doc. 82.2). Notably, the CITES COP's decision not to uplist the lion was influenced by the fact that international trade is not the primary threat faced by the species and that what is needed are consequently not trade bans but cooperative measures between range states (UNEP/CMS/COP12/Doc.24.3.1.3).

CITES, enforcement issues, and the broader lion conservation agenda

As is highlighted by the COP's concerns regarding split-listing, CITES' trade controls clearly cannot be effective unless implemented and enforced (Wandesforde-Smith 2016; Zhou et al. 2016). This is true regardless of the appendix on which a species/population finds itself. Indeed, in 2002 the CITES COP recognized that, despite the Appendix I listing of all Asian big cat species (including the Asiatic lion), illegal trade in these species had escalated and continued to threaten their survival. The COP therefore called for a variety of legislative and enforcement measures to address this situation (Res. Conf. 12.5 (Rev. CoP17)). For Africa's populations of *Panthera leo*, it is worrying that 23 of the range states that are parties to the Convention have been assessed as having inadequate legislation for the effective implementation of CITES (Table 7; see also Watts 2016). Improvements are clearly desirable in this regard, as are measures to enhance the capacity of African states to implement and enforce those laws that do exist (Wandesforde-Smith 2016).

The COP17 decisions on the African lion (Decisions 17.241–245) make no explicit mention of strengthening national CITES-implementation legislation, but call for a wide array of measures to improve the conservation and management of this 'iconic species', many of which are clearly responses to the Entebbe Communiqué. Notably, these CITES COP decisions have also been endorsed by the CMS Standing Committee and will be presented to the CMS COP for adoption in October 2017 (UNEP/CMS/COP12/Doc.24.3.1.3). The decisions direct the CITES Secretariat, subject to external funding and in collaboration with African lion range states, the CMS and the IUCN, to, *inter alia*, 'investigate possible mechanisms to develop and support the implementation of joint lion conservation plans and strategies, taking into consideration existing lion conservation plans and strategies' (the IUCN's 2006 regional Lion Conservation Strategies clearly being significant in this regard); and to take a variety of measures concerning capacity building for joint conservation plans, further international cooperation, ecological and trade research, information-sharing, and education.

Further, the abovementioned decisions direct the CITES Standing Committee to establish a Task Force on African lions, and to consider establishing a trust fund to attract funding for both the work of the Task Force and the implementation of conservation and management plans and strategies for the African lion. Two initiatives which seek to defeat wildlife crime in Africa, and whose participation in, or collaboration with, the African Lion Task Force thus appears to be appropriate, are

Table 7. Status of CITES implementation legislation. Data from http://www.cites.org/eng/legislation, last updated 01/09/2016.

Category	Range state(s)
Category 1 *Believed generally to meet all requirements for effective CITES-implementation*	Cameroon, Democratic Republic of Congo, Ethiopia, Namibia, Nigeria, Senegal, South Africa, Zimbabwe
Category 2 *Believed generally to meet some requirements for effective CITES-implementation*	Benin, Botswana, Burkina Faso, Chad, Guinea, India, Kenya, Malawi, Mali, Mozambique, Sudan, Togo, United Republic of Tanzania, Zambia
Category 3 *Believed generally not to meet any requirements for effective CITES-implementation*	Angola, Central African Republic, Côte d'Ivoire, Ghana, Guinea-Bissau, Niger, Rwanda, Somalia, Swaziland, Uganda
Non-party	South Sudan

the Lusaka Agreement Task Force (established by the 1994 Lusaka Agreement) and the Horn of Africa Wildlife Enforcement Network. Between them, these initiatives presently cover seven lion range states: Ethiopia, Kenya, South Sudan, Sudan, Tanzania, Uganda and Zambia. A final point concerning enforcement is that the 17th CITES COP also adopted a resolution on demand reduction strategies as a means of combatting illegal wildlife trade (Res. Conf. 17.4), prompting some delegates to question whether it is possible to simultaneously reduce demand for illegal products and promote the consumption of legal ones, as the resolution on trophy hunting appears to do (IISD 2016).

Despite its imperfect implementation record and the challenges it faces in balancing calls for preservation with those for sustainable use (Wandesforde-Smith 2016), CITES has a demonstrated potential to make a tangible difference to the conservation of species threatened by trade. For instance, the conservation status of jaguars (*Panthera onca*) and other South American felids notably improved after the CITES ban on trade in their pelts took effect in 1975 (Di Marco et al. 2014). Regarding lions, the least that can be said is that the relevance of CITES to the conservation and sustainable use of the species is likely to stay on the increase for some time to come. However, due to the Convention's narrow focus on trade, and trade not being amongst the primary concerns for lion conservation, CITES provides a necessary but not a sufficient international framework for lion conservation.

Convention on Migratory Species (CMS)

The CMS broadly addresses the conservation of migratory species, and like CITES also lists species in appendices. The Convention supports the conservation and management of migratory species by requiring that parties take specified conservation measures in respect of species in CMS Appendix I; by promoting the development of targeted ancillary instruments, for CMS Appendix II species in particular; and by providing a variety of less formal mechanisms for targeting conservation activity towards particular groups of species or addressing particular cross-cutting threats.

The Convention defines 'migratory species' to mean 'the entire population or any geographically separate part of the population of any species or lower taxon of wild animals, a significant portion of whose members cyclically and predictably cross one or more national jurisdictional boundaries' (Article I(1)(a)). This definition allows the Convention to attach different legal commitments to different populations of the same species, and only encompasses wild animals, thus failing to regulate parties' activities in respect of animals bred in captivity. Further, the CMS COP has taken a remarkably flexible approach in interpreting the definition, having accepted that taxa which periodically traverse (or have historically traversed) national borders are 'migratory species', even if the reason for these movements is simply that their ranges are transboundary (Trouwborst 2012). The lion is a case in point. Moreover, lions can disperse over large distances and some of them migrate along with their migratory prey. In both cases they may traverse international boundaries (UNEP/CMS/COP12/Doc.25.1.3). However, the Asiatic lion currently lacks such transboundary features. At any rate, the COP has explicitly recognised that '*Panthera leo* … and all its evolutionarily significant constituents, including *Panthera leo persica*, satisfy the Convention's definition of "migratory species"' (CMS COP Resolution 11.32, 2014).

Listing lions under the CMS

While CMS Appendix I lists 'endangered' migratory species (Article III(1)), Appendix II is dedicated to migratory species which have an unfavourable conservation status and require international agreements for their conservation and management, as well as species whose conservation status, though not necessarily unfavourable, would significantly benefit from an international agreement (Article IV(1)). At a 2010 meeting of the Convention's Scientific Council, Congo, being interested in CMS support for lion reintroduction efforts, raised the possibility of an Appendix II listing (UNEP/CMS/ScC16REPORT). In 2014, Kenya submitted a proposal to include the Asiatic lion on Appendix I and all other subspecies on Appendix II, which was subsequently revised to propose that all populations of *Panthera leo* be listed on Appendix II (UNEP/CMS/COP11/Doc.24.1.2/Rev.1). Kenya's proposal was ultimately withdrawn, but the COP adopted Resolution 11.32, which *inter alia* requested consultations between range states concerning the population status of *Panthera leo*, and invited range states, subject to the findings of such consultations, to work towards an Appendix II listing proposal to be presented to the 12th CMS COP in October 2017. Subsequently, in the Entebbe Communiqué, range states recognized that the 'CMS can provide a platform to exchange best conservation and management practices; support the development, implementation and monitoring of action plans; promote the standardization of data collection and assessments; facilitate transboundary cooperation; and assist in the mobilization of resources.' Many range states additionally indicated that they would be in favour of an Appendix II listing, although southern African states expressed doubt as to whether their lion populations should be included therein. In accordance with Resolution 11.32, COP12 is indeed set to consider a proposal for listing the lion in Appendix II, which was submitted jointly by Chad, Niger and Togo. The proposal, *inter alia*, describes how lions may cross national jurisdictional boundaries as part of their circadian cycles, life cycles, and annual cycles; and identifies countries which share lion populations that are suspected to cyclically and predictably traverse national boundaries, such that a significant portion of Africa's lion population can be considered 'migratory' for CMS purposes (UNEP/CMS/COP12/Doc.25.1.3).

Support for listing lions on CMS Appendix II has also been expressed in the recent literature (Trouwborst 2015a; Watts 2016), and would certainly fit the pattern of prior CMS practice and recent listing trends. The CMS appendices already include the large carnivore species cheetah and snow leopard (*Panthera uncia*) in Appendix I, and African wild dog and polar bear (*Ursus maritimus*) in Appendix II. The listing proposals that will be considered by CMS COP12 include two further carnivores besides the lion – leopard and Gobi bear (*Ursus arctos isabellinus*) – as well as other African megafauna – chimpanzee (*Pan troglodytes*), giraffe (*Giraffa camelopardalis*) and African wild ass (*Equus africanus*).

In its most recent guidance on assessing proposals to list species on the Convention's appendices, the CMS COP has advised, *inter alia*, that a taxon assessed as 'Extinct in the Wild', 'Critically Endangered', 'Endangered', 'Vulnerable' or 'Near Threatened' using the IUCN Red List criteria satisfies the Convention's definition of 'unfavourable conservation status' and is thus eligible for consideration for Appendix II listing; and that a taxon assessed as falling into one of the first three of these categories is eligible for consideration for listing in Appendix I (Resolution 11.33, 2014). Given their current Red List categorisations, the Asiatic lion and the West African lion are thus eligible for CMS Appendix I listing, while the remainder of *Panthera leo* is eligible for Appendix II listing. Red List status is not, however, the only relevant consideration. The COP has also accepted that listing should only occur if this is expected to result in conservation benefits, and has further highlighted the need to consider listing proposals' 'coherence with existing measures in other multilateral fora' (Resolution 11.33). It is permissible for species to be listed simultaneously in both Appendices I and II (Article IV(2)). Should a species that has only been listed in Appendix II decline to the extent that it becomes endangered, a subsequent Appendix I listing would of course be a possibility – though by no means a certainty given the COP's pragmatic approach to listing. Indeed, 73% of the taxa listed under the Convention appear only in Appendix II (http://www.cms.int/en/species).

At any rate, were any populations of *Panthera leo* to be included in CMS Appendix I, all states belonging to these populations' current range would become subject to certain conservation commitments. Although the Convention does not require that states in which a species is extinct take measures to facilitate its return, any state to which the species is reintroduced or which the species (re)occupies spontaneously will, at that stage, become subject to the same legal requirements as other range states. These include the requirement that states endeavour to take measures to conserve and restore the species' habitat and address factors which impede its migration or otherwise endanger the species (Article III(4)); as well as the requirement that taking of animals belonging to the species be prohibited (Article III(5)). 'Taking' in this context includes 'taking, hunting, ... capturing, harassing, deliberate killing, or attempting to engage in any such conduct' (Article I(1)(i)). On the face of it, the requisite taking prohibition is extremely far reaching, encompassing everything from trophy hunting, to killing for damage control, to capture for the purposes of research or translocation. The Convention does, however, allow for certain exceptions – including for scientific purposes, propagation, traditional subsistence use, or where 'extraordinary circumstances so require' (Article III(5)). These offer CMS parties a measure of flexibility and could conceivably even be relied upon to justify limited trophy hunting, provided that this is strictly controlled and does not operate to the species' disadvantage. That said, the CMS COP has shown a preference for range states in which sustainable taking is possible to request exclusions from Appendix I listing, rather than to rely upon the Convention's exemptions provision (see e.g. Resolution 10.28 on the Saker falcon, *Falco cherrung*). Unsurprisingly, there have thus been instances in which the conservation benefits associated with hunting have been relied upon to argue that Appendix I listing will not be to a population's benefit. For instance, in its assessment of Kenya's proposal to list the African lion on Appendix II, the CMS Scientific Council accepted that, despite the West African lion's IUCN categorisation as Critically Endangered, an Appendix II listing seemed the most appropriate course of action, given stakeholders' belief that a ban on regulated taking would be 'harmful to the conservation of this taxon' (UNEP/CMS/COP11/Inf.8).

Further arguments against certain species' Appendix I listing have been based on the permissibility of trade under CITES. For instance, in 2009, three countries' cheetah populations were excluded from the species' listing on CMS Appendix I because quotas for trade in these populations are permitted under CITES (UNEP/CMS/COP9/REPORT). Including the African lion in CMS Appendix I would not interfere with South Africa's trade in parts from captive-bred animals. However, such uplisting would present difficulties for states which permit trophy hunting of wild lions. Indeed, during the Scientific Council's 2010 discussion of the possibility of listing the African lion in one of the CMS appendices, the CITES representative highlighted that a CMS Appendix I listing would raise similar concerns about CITES-compatibility to those encountered when listing the cheetah (UNEP/CMS/ScC16REPORT). Eight of the lion's range states, including states where trophy hunting is practiced, such as Namibia, are not currently parties to the CMS (Table 2) and therefore would not incur any legal obligations from an Appendix I listing unless they were to ratify the Convention. Caution should therefore be taken to consider the positions of these states when making listing decisions regarding commercially valuable species so as not to *deter* them from becoming parties to the Convention. Notably, Botswana, despite being a non-party, has expressed its support for the CMS Appendix II listing of the African lion (UNEP/CMS/COP12/Doc.25.1.3). Insofar as the Asiatic lion is concerned, a CMS Appendix I listing would in fact *complement* CITES' ban on the commercial trade of animals belonging to this subspecies.

CMS ancillary instruments and lions

While the CMS's substantive conservation requirements only apply in respect of Appendix I species, the Convention also promotes the development of ancillary instruments, which prescribe detailed conservation measures in respect of particular species or groups of species and provide institutional platforms for coordinating, and reviewing progress towards achieving, such measures. Parties to the Convention must endeavour to conclude legally binding 'AGREEMENTS' for the conservation and management of Appendix II species (Article II(3)(c)), giving priority to species with an unfavourable conservation status (Article IV(3)). CMS parties are further encouraged to conclude 'agreements' in respect of taxa whose members 'periodically cross one or more national jurisdictional boundaries' (Article IV(4)). The latter 'agreements', which offer considerably greater flexibility in terms of scope, content and format, have thus far taken the form of either treaties or non-binding memoranda of understanding (MoUs). Institutional structures vary from one instrument to the next, but generally include a management forum (periodic meetings of the parties/signatories), coordination support (whether provided by the CMS Secretariat, an independent Secretariat, or a specific state or non-governmental organization), and some form of scientific/advisory forum (Lee et al. 2010). However, while the legally binding instruments have the stability provided by core funding, the MoUs by contrast depend 'exclusively on voluntary contributions which could be withdrawn or not materialize at any time' (Lee et al. 2010).

Were *Panthera leo* or any of its populations to be listed on Appendix II, it would be possible and in accordance with the Convention to develop a binding AGREEMENT, whose membership would be open to all range states, regardless of whether they are CMS parties (Article V(2)). Such an instrument could potentially also incorporate other large carnivores with overlapping ranges – the African wild dog being an especially obvious candidate, given its current Appendix II listing and unfavourable conservation status (Trouwborst 2015a). Alternatively – and *regardless* of whether the lion is ultimately listed on either of the CMS appendices – Article IV(4) would allow the development of a treaty or MoU focused either exclusively on lions or more broadly on the conservation and management of transboundary large carnivore populations throughout Africa and/or Asia (or portions thereof).

On the one hand, there are distinct advantages to providing such a formal, high-profile and permanent platform in the form of an ancillary instrument, and doing so would be in line with the Convention's provisions. On the other hand, the development and functioning of a new ancillary instrument entails administrative and financial burdens. As with any international legal instrument, this can be expected to influence states' willingness both to initiate the development of, and become parties or (in the case of an MoU) signatories to, such an instrument. Given the urgent need to direct resources towards *in situ* conservation efforts, states are likely to be especially hesitant to develop a new instrument, with an independent administrative and/or decision-making structure, if they consider it possible to achieve their objectives under existing legal and institutional frameworks. Indeed, in the face of resource constraints, the CMS COP has recognized the need to avoid an unwarranted proliferation of ancillary instruments and has adopted criteria against which to assess proposals for the development of new instruments (Resolution 11.12, 2014). One such criterion, quite sensibly, is the absence of superior alternatives – either outside the CMS system or within it.

CMS Concerted Actions and lions

One type of alternative remedy within the CMS system is the establishment, through resolution, of 'Concerted Actions' to improve the conservation status of specified Appendix I and II species, the implementation of which is monitored by the Convention's Scientific Council (Resolution 10.23, 2011). Concerted Actions may operate on a single- or multi-species basis and the COP has accepted that they may act as either a precursor or alternative to the conclusion of a dedicated treaty or MoU (Resolution 11.13, 2014). The Scientific Council has recognized that, if listed on either of the CMS appendices, the lion would be an appropriate species for Concerted Action (UNEP/CMS/COP11/Inf.8).

In addition, portions of the lion's present and historic range are already encompassed by two existing, geographically-based, multi-species Concerted Actions: the Sahelo-Saharan Megafauna Concerted Action and the Central Eurasian Aridland Mammals Concerted Action. The species on which these Concerted Actions are initially centred include two species of large carnivores – snow leopard and cheetah – and the COP's intention is that they 'will in due course cover all threatened migratory large mammals of the temperate and cold deserts, semi-deserts, steppes and associated mountains' of the Sahelo-Saharan region and Central Eurasia (Recommendations 9.1 and 9.2, 2008). Importantly for the Asiatic lion, the COP has requested the Scientific Council and the Secretariat to 'ensure that all means that can effectively contribute to an improvement of the conservation status of Asian big cats and to awareness raising on the threats they face are taken within the framework of the Central Eurasian Aridland Mammals Concerted Action' (Recommendation 9.3, 2008). Lion populations not falling within the geographic scope of the existing multi-species Concerted Actions could theoretically be covered by a Sub-Saharan Megafauna Concerted Action, the establishment of which has already been identified as a possibility by the CMS Scientific Council (UNEP/CMS/COP11/Inf.8).

CMS Action Plans, Special Species Initiatives and lions

Species action plans can play a key role in operationalizing Concerted Actions. However, such plans can also be developed, or existing plans endorsed (the regional Lion Conservation Strategies being potential candidates), within other contexts within the CMS regime. So can international working groups to monitor and support their implementation. A further available mechanism takes the form of 'Special Species Initiatives', the prime example being the Central Asian Mammals Initiative (CAMI). The CAMI and its associated Programme of Work, the implementation of which is coordinated by the CMS Secretariat, act as a common strategic framework for action, drawing together the various CMS instruments and mandates of relevance to the species involved (Resolution 11.24, 2014). The establishment, in collaboration with the CITES Secretariat, of a similar initiative for African carnivores will be proposed at this year's CMS COP. It is envisaged that this Joint CMS-CITES African Carnivores Initiative will be used to develop both 'concrete, coordinated and synergistic conservation programmes' and 'policy guidance and recommendations'; and to 'organize the collaboration with other conservation initiatives and organizations' (UNEP/CMS/COP12/Doc.24.3.1.1). While the CAMI focuses primarily on Concerted Action species, four of the 15 species it covers are not listed on the CMS Appendices. This suggests that it would be possible for the Asiatic lion to be incorporated into the Initiative, even without CMS listing. It similarly suggests the possibility of the anticipated African Carnivores Initiative to encompass not only listed, but also non-listed species.

Flexibility and limited resource demands are amongst the advantages of Concerted Actions and Special Species Initiatives, and securing the initial participation of states may also be easier than with a binding ancillary instrument. Conversely, compared to an ancillary treaty, it may be harder to maintain states' commitment and to monitor implementation over time, due to a lack of core funding, a dedicated institutional structure and 'legal teeth'.

As a final and more general point, whereas it is clear from the above that the CMS regime offers certain options for directing conservation action towards *non*-listed species, listing the lion on either or both of the Convention's appendices would raise the species' profile and would significantly increase the likelihood of lions being afforded priority within the Convention's busy agenda. Indeed, the CMS Secretariat has observed that it may not be justifiable to dedicate the Convention's limited resources to supporting the conservation of an unlisted species (UNEP/CMS/COP12/Doc.24.3.1.3).

Convention on Biological Diversity (CBD)

All 33 lion range states are contracting parties to the CBD, which aims broadly for the conservation and sustainable use of biological diversity, including at the ecosystem, species and genetic level. The Convention lacks lists of species requiring special attention. Regardless, many of the duties it spells out are of plain relevance to lions. These include obligations regarding national biodiversity strategies, plans or programmes (Article 6), *in-situ* conservation (Article 8), sustainable use (Article 10) and environmental impact assessment (Article 14). To single out one of these, Article 8 requires each party, 'as far as possible and as appropriate', *inter alia* to establish a 'system of protected areas or areas where special measures need to be taken to conserve biological diversity', '[p]romote the protection of ecosystems, natural habitats and the maintenance of viable populations of species in natural surroundings', '[r]ehabilitate and restore degraded ecosystems and promote the recovery of threatened species', and '[d]evelop or maintain necessary legislation and/or other regulatory provisions for the protection of threatened species and populations'. Whereas the above provisions are just as binding as other treaty obligations, they are phrased in such a broad and qualified manner that it is difficult in practice to identify the boundary between compliance and violation. Parties evidently dispose of an ample margin to determine what, in their individual circumstances, is 'possible' and 'appropriate', although this discretion is not limitless. For instance, allowing a species to go extinct on its territory is clearly hard to reconcile with a state's obligations under the CBD.

For present purposes, the CBD is also of significance as a high-profile forum for signaling, discussing, and sharing information and experience regarding all manner of conservation issues; as a catalyst for mainstreaming the consideration of biodiversity into broader policy agendas; and as a source of non-binding but authoritative guidance as developed and endorsed by the CBD COP. Most of the strategic 'Aichi Biodiversity Targets' adopted by the COP in 2010, for instance, are relevant to lion conservation, such as the 12th: 'By 2020 the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained' (CBD Strategic Plan for Biodiversity 2011–2020). Also of evident relevance are the 2004 'Addis Ababa Principles and Guidelines for the Sustainable Use of Biodiversity', according to which it is 'possible to use biodiversity components in a manner in which ecological processes, species and genetic variability remain above thresholds needed for long-term viability,' while 'all resource managers and users have the responsibility to ensure that use does not exceed these capacities' (CBD COP Decision VII/12, 2004).

Given the threat posed by depletion of lions' prey base, the CBD's active role in addressing the unsustainable use of bushmeat is particularly relevant. The Convention's Liaison Group on Bushmeat has developed specific recommendations to complement the Addis Ababa Principles and Guidelines in this regard, which have been endorsed by the CBD COP (CBD COP Decisions XI/25, 2012, and XII/18, 2014), and also by the CITES COP (Res. Conf. 13.11(Rev. CoP17)). The CBD COP has urged parties to develop and promote methods and systems, and build capacity and community awareness 'to determine sustainable wildlife harvest levels at national and other levels, with a particular view to monitoring and improving sustainable wildlife management and customary sustainable use,' and to develop and promote 'sustainable alternatives to the unsustainable use of wildlife' (CBD COP Decision XI/25, 2012). Bushmeat is furthermore addressed in a volume of the CBD Technical Series (Nasi et al. 2008) and, pursuant to COP Decision XI/25, a Collaborative Partership on Sustainable Wildlife Management (CPW) was established, which has developed a sourcebook on bushmeat. Notably, the CPW's 14 members include both CITES and the CMS, and the latter's 2017 COP will consider the adoption of several draft decisions on addressing the unsustainable use of wild meat (UNEP/CMS/COP12/Doc.24.4.7).

Regional instruments

In addition to the global conventions considered above, here we summarize several relevant regional agreements, although we stress that this concise treatment does not necessarily reflect a lesser practical importance of these instruments to lions.

African Convention

The 1968 African Convention, administered by the African Union, is in force for 21 lion range states (Table 2). Notably, Botswana, Namibia, South Africa and Zimbabwe are not amongst its contracting parties. The lion – alongside six other large carnivores – is listed as a protected species in the Annex to the Convention. Consequently, contracting parties are under an obligation to ensure that lions are 'totally protected' throughout their territories, which includes prohibiting their hunting, killing and capture (Article VIII). As lions are subject to the flexible 'Class B' regime, this prohibition may be lifted 'under special authorization' at the discretion of the 'competent authority'. The Convention places restrictions on certain means of capture and killing, including a prohibition on the use of poisoned baits (Article VII). Trade in lions and lion trophies must be regulated, and their export, import and transit made subject to an authorization 'which shall not be given unless the specimens or trophies have been obtained legally' (Article IX). Regarding lion habitat, the Convention requires parties to maintain, expand and/or newly establish 'conservation areas' – a term covering 'strict nature reserves', 'national parks' and 'special nature reserves' – so as to 'ensure conservation of all species and more particularly of those listed … in the annex' (Article X(1)). Concerning the peripheries of such protected areas, parties 'shall establish, where necessary, around the borders of conservation areas, zones within which the competent authorities shall control activities detrimental to the protected natural resources' (Article X(2)).

The African Convention appears to have contributed to the increase in protected areas and improvements in national hunting and wildlife trade legislation in many lion range states during the years following the Convention's adoption (Bowman et al. 2010). Unfortunately, however, the failure of the Convention's drafters to establish a COP or similar institutional framework to oversee and promote implementation and enforcement has made the 1968 African Convention something of a 'sleeping treaty'

(Bowman et al. 2010). A substantially revised version of the Convention – including an institutional framework but lacking a species-specific focus – was negotiated in 2003, but requires a further two ratifications to enter into force.

Bern Convention

The Bern Convention, the Council of Europe's counterpart of the African Convention, is something of an oddity in the current review. Notwithstanding its primary focus on European wildlife, as reflected in its title, in certain ways the geographic scope of the Convention extends beyond Europe. Without going into the particulars (see Bowman et al. 2010), we note here that the Bern Convention has a small number of African states parties, including two lion range states, Burkina Faso and Senegal. The lion itself is not listed under the Convention – although leopard, tiger (*Panthera tigris*) and dhole (*Cuon alpinus*) are (see also Trouwborst 2017). Still, it would seem that the general obligation in Article 2 of the Bern Convention requires Burkina Faso and Senegal to 'take requisite measures to maintain the population of [lions] at, or adapt it to, a level which corresponds in particular to ecological, scientific and cultural requirements' – i.e., a level at which the population is not threatened with extinction (Bowman et al. 2010; Trouwborst et al. 2017b). Interestingly, in 2005 the Standing Committee (the Bern Convention's COP equivalent) called for increased international cooperation regarding transboundary populations of large carnivores, including: 'Lion (*Felis leo*) and leopard (*Panthera pardus*) in the National Park of Niokolo Koba (Senegal) and Mali' (Standing Committee Recommendation No. 115, 2005). Overall, however, the relevance of the Bern Convention to lion conservation appears to have been marginal at best, and there are no indications for this to radically change in the foreseeable future.

SADC Protocol on Wildlife Conservation and Law Enforcement

The SADC covers the large region from the tip of South Africa to the DRC and Tanzania in the north. The SADC Protocol on Wildlife Conservation and Law Enforcement is currently in force for eight lion range states (Table 2), and could in future apply to a further three range states once they ratify (Angola, DRC, Swaziland). The Protocol is intended to provide 'common approaches to the conservation and sustainable use of wildlife resources and to assist with the effective enforcement of laws governing these resources' (Article 4(1)), whereby 'wildlife' is defined as 'animal and plant species occurring within natural ecosystems and habitats' (Article 1). Some of the Protocol's specific objectives are to promote sustainable wildlife use; harmonize relevant legal instruments; assist in national and regional capacity-building for wildlife conservation, management and law enforcement; facilitate community-based management practices; and to promote conservation of shared wildlife populations through the establishment of TFCAs (Article 4(2)). To achieve these objectives, the Protocol lays down a range of obligations, accompanied by an institutional framework. The latter includes a Committee of Ministers, a Committee of Senior Officials, a Technical Committee composed of the Directors of countries' wildlife agencies, and a 'Wildlife Sector Technical Coordinating Unit' acting as Secretariat (Article 5).

Whereas the Protocol does not contain species-specific provisions, many obligations are of significance from a lion conservation perspective. For instance, each contracting party 'shall ensure the conservation and sustainable use of wildlife resources under its jurisdiction' (Article 3(1)). To that end, parties 'shall adopt and enforce legal instruments' (Article 6(1)) and 'assess and control activities which may significantly affect the conservation and sustainable use of wildlife so as to avoid or minimise negative impacts' (Article 7(2)). Parties shall take measures to 'ensure the maintenance of viable wildlife populations' and prevent over-exploitation, including by regulating the taking of wildlife through 'restrictions on the number, sex, size or age of specimens taken and the locality and season during which they may be taken' (Article 7(3)). Regarding transboundary populations, parties shall, as appropriate, 'establish programmes and enter into agreements to promote the co-operative management of shared wildlife resources and wildlife habitats across international borders' (Article 7(5), and generally 'promote the development of transfrontier conservation and management programmes' (Article 7(9)). Likewise, parties are to 'endeavour to harmonise national legal instruments governing the conservation and sustainable use of wildlife resources' (Article 6). A particularly important instrument to further the coordination and harmonization of the management of transboundary wildllfe populations and ecosystems is the establishment of TFCAs (discussed below). Lastly, we highlight the development of thematic international strategies developed within the framework of the SADC Protocol, such as the SADC Law Enforcement and Anti-Poaching Strategy 2016–2021.

In sum, the relevance of the Protocol to ensuring conservation and sustainable use of lions in the SADC region is evident. We do draw attention to the difficulties involved in implementing the various objectives and obligations in the Protocol. For instance, the transboundary harmonization of legislation can be quite a challenge, as illustrated by the analysis conducted by Selier et al. (2016) regarding the management of a trilateral elephant population in the SADC region.

Treaties establishing Transfrontier Conservation Areas

Some particularly significant treaties from a lion conservation viewpoint have a modest geographic scope. These are the bilateral or trilateral treaties establishing TFCAs, although one exceptional treaty involves five parties. Four treaty-based TFCAs of importance to lions are:

Kgalagadi (Botswana, South Africa)
Great Limpopo (Mozambique, South Africa, Zimbabwe)
Kavango Zambezi (Angola, Botswana, Namibia, Zambia, Zimbabwe)
Malawi-Zambia (Malawi, Zambia)

Another four TFCAs of actual or potential importance to lion conservation are as yet based only on MoUs:

Lubombo (Mozambique, South Africa, Swaziland)
Iona Skeleton Coast (Angola, Namibia)
Greater Mapungubwe (Botswana, South Africa, Zimbabwe)
Chimanimani (Mozambique, Zimbabwe)

TFCAs which are still to be formalized include:

Liuwa Plains-Mussuma (Angola, Zambia),
Lower Zambezi-Mana Pools (Zambia, Zimbabwe)
ZiMoZa (Mozambique, Zambia, Zimbabwe)
Kagera (Rwanda, Tanzania, Uganda)
Niassa-Selous (Mozambique, Tanzania)
Mnazi Bay-Quirimbas (Mozambique, Tanzania)

(For the latest developments regarding each TFCAs, see http://www.peaceparks.org.)

For illustrative purposes, we discuss one TFCA treaty, selecting the most spectacular one. In 2011, the presidents of Angola, Botswana, Namibia, Zambia and Zimbabwe concluded the Treaty on the Establishment of the Kavango Zambezi Transfrontier Conservation Area (KAZA TFCA), which entered into force a year later. The resulting TFCA encompasses and unites a huge array of pre-existing protected areas and multiple resource use areas in the five countries, many of which are important lion areas, and currently covers approximately 520,000 km^2 – roughly the size of France. While duly recognizing its ties with the SADC (Article 9), the Treaty formally established the KAZA TFCA as an autonomous 'international organisation' with legal personality (Article 3), and headquarters in Kasane (Article 2). The Treaty set up various institutions charged with administering and further developing the KAZA TFCA, including a Ministerial Committee, Committee of Senior Officials, Joint Management Committee, Secretariat and National Committees (Articles 10-23; see also http://www.kavangozambezi.org).

The KAZA TFCA aims to 'maintain and manage' the shared natural resources and biodiversity of the area to 'support healthy and viable populations of wildlife species', and to develop a 'complementary network of Protected Areas within the KAZA TFCA linked through corridors to safeguard the welfare and continued existence of migratory wildlife species' (Article 6(1)). Other objectives of relevance to lions are to transform the TFCA into a 'premier tourist destination in Africa'; to enhance the sustainable use of natural resources to improve human livelihoods and reduce poverty; to 'promote and facilitate the harmonisation of relevant legislation, policies and approaches'; and to 'ensure compliance with international protocols and conventions related to the protection and Sustainable Use of species and ecosystems' (Article 6(1)).

The general principles that the five states are expected to uphold in their pursuit of these objectives include the recognition that the right to utilize natural resources 'carries with it the obligation to do so in a responsible manner so as to ensure effective Conservation and management for posterity;' to ensure that wildlife use is sustainable; to rehabilitate declining populations; and generally to take 'knowledge based decisions derived from interdisciplinary research and traditional knowledge and to exercise precaution when there is insufficient information' (Article 5). The five partner states are under obligations to 'ensure the protection and management of those parts of the Kavango Zambezi ecosystem falling directly under their jurisdiction;' to cooperate in developing common approaches to *inter alia* wildlife management and tourism; and to ensure proper stakeholder engagement at national and local levels (Article 8).

In sum, investing in the implementation of existing TFCA treaties and the adoption of treaties for further areas can evidently be beneficial for lion conservation and sustainable use. Consolidating the Niassa-Selous TFCA would seem particularly important, as this area hosts the largest lion population, estimated at over 5,000 lions (Dickman et al. submitted).

Discussion and recommendations

The above review reveals a significant body of international wildlife law of relevance to the conservation and sustainable use of lions. Moreover, it reveals a significant potential for enhancing the contribution of wildlife treaties in this regard. The time is right to invest in such improvements, and our analysis renders several general and treaty-specific recommendations for doing so. Some of the most significant are provided below.

It is appropriate to place our findings in perspective by noting that no number or combination of relevant treaties can by themselves secure the conservation of lions into the long-term future. International wildlife law provides one set of tools in a much larger toolkit comprising a range of other approaches, mechanisms and disciplines, many of which are likely to be needed.

Implementation and participation

It seems safe to assume that the future of lions would be much more secure if all range states fully lived up to the international obligations identified in the above analysis. However, the implementation of these obligations is affected by pervasive compliance deficiencies due to problems of capacity, governance and enforcement in many range states (Dickman et al. 2015; Dickman et al. submitted). All efforts aimed at decreasing these deficiencies and improving compliance are thus to be encouraged.

Figure 3 shows a summary of Dickman et al's (submitted) index of infrastructural fragility for the 33 lion range states. In brief, this index is based on a set of socio-political, habitat and conservation variables that are likely to influence the success of conservation measures to secure lions within each range state. Thus, the geopolitical

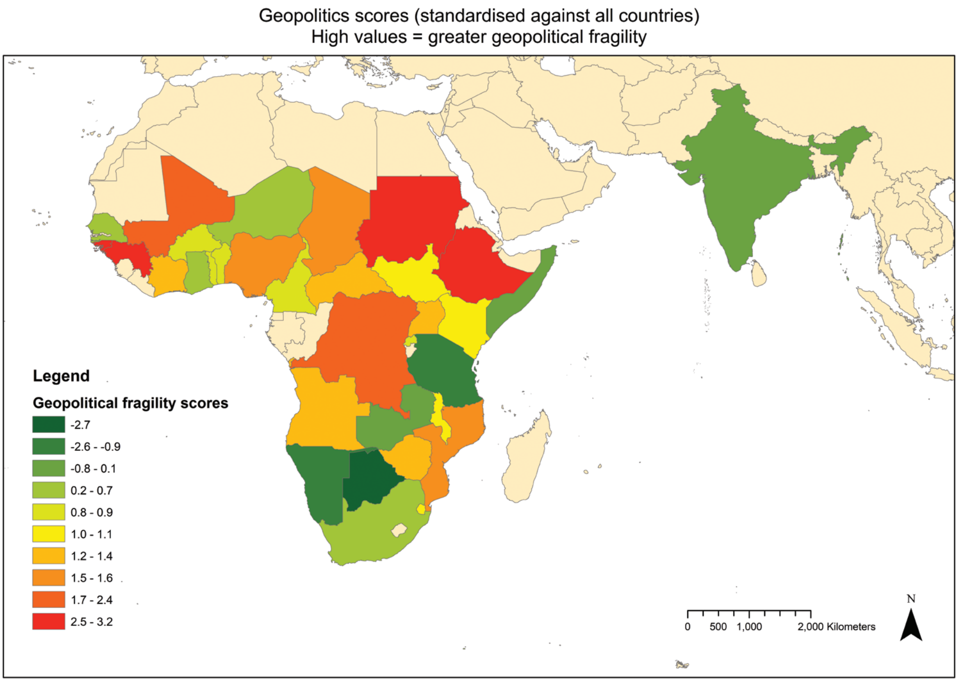

Figure 3. The map shows the geopolitical values of lion range states, where higher values represent greater fragility in the infrastructure of the state (based on Dickman et al., submitted).

score is the sum of standardized (relative to the average of the sample states), national-level data on factors including: the level of political corruption, stability and regulatory quality (governance metrics), measures of economic development (GDP and the Human Development Index), human population growth and density (factors that put pressure on available lion habitat) and the percentage of land designated as protected area (conservation).

Depending on the particular circumstances and the treaty obligation(s) involved, there is a time and a place for top-down as well as bottom-up approaches, for coercive as well as flexible approaches, and for all manner of combinations of these (Treves et al. 2017; Chapron et al. 2017; Redpath et al. 2017). It is important to note in this regard that the participation of local and indigenous communities, poverty alleviation, awareness raising and education have become key features in the implementation of all the major conservation treaties, as expressed in COP decisions, strategies, funding allocations, and guidance documents (see, e.g., Ramsar Convention Secretariat 2010; CBD Secretariat 2011; UNESCO et al. 2012).

Another generic issue is that of participation gaps at the intergovernmental level. The utility of some treaties to lions could be improved through the accession of range states that are still missing as contracting parties, such as Botswana, Namibia and Zambia in the case of the CMS. Further participation gaps are indicated in Table 2.

Site-based treaties

For sites of importance to lions that are listed under the Ramsar and/or World Heritage Convention, it is clearly worthwhile to take advantage of that international status in order to improve site management and avert harmful human impacts, as appropriate. The opportunities to do so are wide-ranging, varying from the Conventions' funding schemes to litigation, and will generally be greatest for sites where lions were part of the official motivation for listing. The possibility of listing on the Montreux Record and/or List of World Heritage in Danger can also provide useful leverage. For listed sites from which lions have disappeared we recommend not losing sight of lions in site management but rather enabling and working towards their future return, in particular by conserving their habitat and prey base.

Likewise, there is clear merit in working towards the listing of additional sites of importance to lions under either Convention. For the World Heritage Convention, range states' tentative lists would be the natural starting point in this connection (see Table 5 for candidates), although some important candidate sites are not yet on these lists – Tanzania's Ruaha National Park being a case in point. Significantly, the listing of transboundary sites is eligible under both the Ramsar and the World Heritage Conventions. The proper conservation and management of transboundary sites for lions can evidently also benefit substantially from their designation as a TFCA through a dedicated treaty. Such a TFCA agreement can also assist in implementing applicable international obligations under other instruments for the sites in question. The consolidation of the Niassa-Selous TFCA is of particular importance from a lion conservation perspective.

Generally, the more international designations a site has, the better its chances of survival and appropriate management. Ramsar designation is easier to achieve than World Heritage listing, although once achieved the latter status is of a higher legal caliber (and is available for a broader range of habitats). Ramsar designation can also be an intermediate step towards ultimate World Heritage listing.

Both for existing and potential future sites with an international designation, it is essential to address the unsustainable killing of lions and their prey not only within but also around the borders of those sites, and to avoid simply relocating human-lion conflict to the sites' peripheries.

Species-based treaties

CITES provides a necessary framework for trade-related threats to lions and there remains scope to strengthen the Convention's restrictions, as necessary, either by uplisting African lion populations to Appendix I or adding further annotations to the current Appendix II listing. If established, the joint CITES-CMS African Carnivores Initiative will provide an opportunity to address problems affecting implementation. However, CITES does not provide sufficient mechanisms for addressing threats other than trade.

Regarding the CMS, our review indicates that there is definite scope and need for reinforcement and coordination of actions to further lion conservation and sustainable use across the species' range. All the other treaties we reviewed appear to be of actual or potential use in this regard, and sometimes contribute crucial pieces of the puzzle. Yet, all of them are subject to limitations. The Ramsar Convention is limited to wetlands; the WHC is limited to sites of outstanding universal value; CITES is limited to international trade; the CBD is very general and lacks a species-specific focus; the African Convention is institutionally dormant and several important range states are not parties; the Bern Convention is of marginal significance; the SADC Protocol has a limited geographic scope and lacks a species-specific focus; and the various TFCA treaties have geographically limited and fragmented scopes, and remain conceptual in some of the most significant habitats for lions. Given the fragmented collection of treaties which currently apply to lions and the absence of adequate international instruments and/or institutions for lion conservation in at least portions of the species' range, an important role appears, in principle, to be reserved for the CMS, both in terms of coordination and gap-filling. Listing lions under the Convention would be a logical step in this regard, and our analysis provides strong support for doing so.

The species' currently proposed listing on Appendix II would both signal the need to develop more elaborate species-specific frameworks for lion conservation and sustainable use and increase the avenues available for achieving this. Should CMS COP12 decide to list the lion or any of its populations on the CMS Appendices, it would further seem sensible for the COP to designate lions for Concerted Action – whether this be as a precursor to the eventual development of an ancillary instrument or as an alternative thereto. Concerted Action for the Asiatic lion could, in principle, be implemented by including this subspecies in CAMI. For Africa, the proposed CMS-CITES African Carnivores Initiative has the potential to enhance coordination and collaboration amongst existing conservation initiatives and instruments throughout the African lion's range and could play an especially pronounced role in subregions which lack alternative treaty mechanisms to support transboundary cooperation and national implementation. Indeed, the establishment of coordination and support mechanisms under the CMS should, in principle, assist range states to implement legal commitments which they have long held under other international instruments (such as the African Convention), regardless of whether or not they at some stage decide to undertake *new* legal commitments through CMS Appendix I listing or the development of an ancillary treaty.

Concluding observations

With their long-term, legally binding commitments on a transboundary scale; their high profiles; their platforms for cooperation and coordination; and various support mechanisms, international treaties have a distinct contribution to make to lion conservation. The above review makes clear what can and cannot be expected of international wildlife law in this regard. Importantly, our review shows that there is still much to be gained, partly by advancing the effective implementation of the currently applicable law in the diverse and often challenging domestic contexts of the various lion range states, and partly by enhancing the legal framework itself.

At the intergovernmental level, listing lions under the CMS can be expected to render particular advantages in terms of the coordination and facilitation of lion conservation action across the species' range. Other recommendations flowing from our analysis include making optimal use of the World Heritage and Ramsar Conventions, CITES and TFCA treaties for lion conservation. Overall, in order to maximize range states' compliance with their international commitments concerning lions, the development and implementation of participatory conservation strategies adjusted to national and local circumstances appears crucial.

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References

Abade L, Macdonald DW, Dickman AJ (2014) Assessing the relative importance of landscape and husbandry factors in determining large carnivore depredation risk in Tanzania's Ruaha landscape. Biological Conservation 180: 241–248. https://doi.org/10.1016/j.biocon.2014.10.005

Arthur E (2014) Poaching cultural property: invoking cultural property law to protect elephants. Journal of International Wildlife Law and Policy 17: 231–253. https://doi.org/10.1080/13880292.2014.957029

Bauer H, Nowell K, Breitenmoser U, Jones M, Sillero-Zubiri C (2015) Review of Lion Conservation Strategies. UNEP/CMS.

Bauer H, Packer C, Funston PF, Henschel P, Nowell K (2016) Panthera leo. The IUCN Red List of Threatened Species 2016: e.T15951A107265605. https://doi.org/10.4337/9781781004791.00008

Bertzky B (2014) World Heritage and species: safe havens for wildlife? World Heritage 73: 30–39.

Bowman M (2016) Law, legal scholarship and the conservation of biological diversity: 2020 vision and beyond. In: Bowman M, Davies P, Goodwin E (Eds) Research handbook on biodiversity and law. Edward Elgar, Cheltenham, 3–54.

Bowman M, Redgwell C, Davies P (2010) Lyster's International Wildlife Law. 2nd ed. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511975301

Breitenmoser U, Mallon DP, Ahmad Khan J, Driscoll C (2008) Panthera leo ssp. persica. The IUCN Red List of Threatened Species 2008: 3.T15952A5327221.

Caro TM (2003) Umbrella species: critique and lessons from East Africa. Animal Conservation 6: 171–181. https://doi.org/10.1017/S1367943003003214

CBD Secretariat (2011) Livelihood alternatives for the unsustainable use of bushmeat. CBD Secretariat, Montreal.

Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM (2015) Accelerated modern human-induced species losses: entering the sixth mass extinction. Science Advances 1: e1400253. https://doi.org/10.1126/sciadv.1400253

Chapron G, Kaczensky P, Linnell JDC, von Arx M, Huber D, Andrén H, López-Bao JV, Adamec M, Álvares F, Anders O, Balčiauskas L, Balys V, Bedő P, Bego F, Blanco JC, Breitenmoser U, Brøseth H, Bufka L, Bunikyte R, Ciucci P, Dutsov A, Engleder T, Fuxjäger C, Groff C, Holmala K, Hoxha B, Iliopoulos Y, Ionescu O, Jeremić J, Jerina K, Kluth G, Knauer F, Kojola I, Kos I, Krofel M, Kubala J, Kunovac S, Kusak J, Kutal M, Liberg O, Majić A, Männil P, Manz R, Marboutin E, Marucco F, Melovski D, Mersini K, Mertzanis Y, Mysłajek RW, Nowak S, Odden J, Ozolins J, Palomero G, Paunović M, Persson J, Potočnik H, Quenette P-Y, Rauer G, Reinhardt I, Rigg R, Ryser A, Salvatori V, Skrbinšek T, Stojanov A, Swenson JE, Szemethy L, Trajçe A, Tsingarska-Sedefcheva E, Váňa M, Veeroja R, Wabakken P, Wölfl M, Wölfl S, Zimmermann F, Zlatanova D, Boitani L (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346: 1517–1519. https://doi.org/10.1126/science.1257553

Chapron G, Epstein Y, Trouwborst A, López-Bao JV (2017) Bolster legal boundaries to stay within planetary boundaries. Nature Ecology & Evolution 1: 0086. https://doi.org/10.1038/s41559-017-0086

Cliquet A, Backes C, Harris J, Howsam P (2009) Adaptation to climate change: legal challenges for protected areas. Utrecht Law Review 5: 158–175. https://doi.org/10.18352/ulr.100

Department of Environmental Affairs (2017) Lion export quota for 2017 communicated to the CITES Secretariat in line with CITES requirements. http://www.gov.za/speeches/lion-export-quota-2017-communicated-cites-secretariat-line-cites-requirements-28-jun-2017 [accessed: 28 June 2017]

Dickman AJ, Hinks AE, Macdonald EA, Burnham D, Macdonald DW (2015) Priorities for global felid conservation. Conservation Biology 29: 854–864. https://doi.org/10.1111/cobi.12494

Dickman A, Hinks A, Riggio J, Jacobson A, Loveridge A, Macdonald E, Burnham D, Bauer H, Funston P, Henschel P, Hunter L, Jacobsen K, Lindsey P, Packer C, Silero C, Macdonald DW (submitted) Ecological and socio-political fragility of free-ranging African lion populations. Submitted to Conservation Biology.

Di Marco M, Boitani L, Mallon D, Hoffmann M, Iacucci A, Meijaard E, Visconti P, Schipper J, Rondinini C (2014) A retrospective evaluation of the global decline of carnivores and ungulates. Conservation Biology 28: 1109–1118. https://doi.org/10.1111/cobi.12249

Di Minin E, Slotow R, Hunter LTB, Montesino Pouzols F, Toivonen T, Verburg PH, Leader-Williams N, Petracca L, Moilanen A (2016) Global priorities for national carnivore conservation under land use change. Scientific Reports 6: 23814. https://doi.org/10.1038/srep23814

Epstein Y, López-Bao JV, Chapron G (2016) A legal-ecological understanding of favorable conservation status for species in Europe. Conservation Letters 9: 81–88.

European Commission (2016) Larger than elephants: inputs for an EU strategic approach to wildlife conservation in Africa – regional analysis. Directorate-General for International Cooperation and Development, Brussels. https://doi.org/10.1111/conl.12200

Gardner RC, Connolly KD, Bamba A (2009) African Wetlands of International Importance: assessment of benefits associated with designations under the Ramsar Convention. Georgetown International Environmental Law Review 21: 257–294.

Gillespie A (2011) Conservation, biodiversity and international law. Edward Elgar, Cheltenham. https://doi.org/10.4337/9780857935168

Hance J (2016) Cecil's legacy: could the death of one lion start a conservation movement? The Guardian. [accessed: 27 April 2016]

Henschel P, Coad L, Burton C, Chataigner B, Dunn A, Macdonald D, Saidu Y, Hunter L (2014) The lion in West Africa is critically endangered. Plos ONE 9: e83500. https://doi.org/10.1371/journal.pone.0083500

Henschel P, Bauer H, Sogbohoussou E, Nowell K (2015) Panthera leo (West Africa subpopulation). The IUCN Red List of Threatened Species 2015: e.T68933833A54067639.

HSBC (2014) World Heritage Sites and Ramsar Wetlands Policy. HSBC.

IISD (2016) Summary of the Seventeenth Meeting of the Conference of the Parties to the Convention on International Trade in Endangered Species of Wild Fauna and Flora: 24 September – 4 October 2016. Earth Negotiations Bulletin 21: 97.

IUCN (2006a) Conservation Strategy for the Lion in West and Central Africa. IUCN SSC Cat Specialist Group, Yaounde.

IUCN (2006b) Conservation Strategy for the Lion in East and Southern Africa. IUCN SSC Cat Specialist Group, Johannesburg.

Lee R, Filgueira B, Caddell R, Frater L (2010) Review of the current organization and activities of CMS and the CMS family: first step of the inter-sessional future shape process. UNEP/CMS/Inf.10.14.8.

Lewis MG (2009) CITES and rural livelihoods: the role of CITES in making wildlife conservation and poverty reduction mutually supportive. Journal of International Wildlife Law and Policy 12: 248–275. https://doi.org/10.1080/13880290903433014

Lindsey PA, Petracca LS, Funston PJ, Bauer H, Dickman A, Everatt K, Flyman M, Henschel P, Hinks AE, Kasiki S, Loveridge A, Macdonald DW, Mandisodza R, Mgoola W, Miller SM, Nazerali S, Siege L, Uiseb K, Hunter LTB (2017) The performance of African protected areas for lions and their prey. Biological Conservation 209: 137–149. https://doi.org/10.1016/j.biocon.2017.01.011

Loveridge AJ, Wang SW, Frank LG, Seidensticker J (2010) People and wild felids: conservation of cats and management of conflicts. In: Macdonald DW, Loveridge AJ (Eds) Biology and conservation of wild felids. Oxford University Press, Oxford, 161–196.

Loveridge AJ, Valeix M, Chapron G, Davidson Z, Mtare G, Macdonald DW (2016) Conservation of large predator populations: demographic and spatial responses of African lions to the intensity of trophy hunting. Biological Conservation 204: 247–254. https://doi.org/10.1016/j.biocon.2016.10.024

Macdonald DW (2016) Report on lion conservation with particular respect to the issue of trophy hunting. Commissioned by UK Under Secretary of State for the Environment. WildCRU, University of Oxford, Oxford.

Macdonald DW, Burnham D, Hinks AE, Wrangham R (2012) A problem shared is a problem reduced: seeking efficiency in the conservation of felids and primates. Folia Primatologica 83: 171–215. https://doi.org/10.1159/000342399

Macdonald DW, Boitani L, Dinerstein E, Fritz H, Wrangham R (2013) Conserving large mammals. In: Macdonald DW, Willis KJ (Eds) Key topics in conservation biology 2. Wiley-Blackwell, Oxford, 277–311. https://doi.org/10.1002/9781118520178.ch16

Macdonald EA, Burnham D, Hinks A, Dickman AJ, Yadvinder M, Macdonald DW (2015) Conservation inequality and the charismatic cat: *Felis felicis*. Global Ecology and Conservation 3: 851–866. https://doi.org/10.1016/j.gecco.2015.04.006

Macdonald DW, Jacobsen KS, Burnham D, Johnson PJ, Loveridge AJ (2016) Cecil: a moment or a movement? Analysis of media coverage of the death of a lion, *Panthera leo*. Animals 6: 26. https://doi.org/10.3390/ani6050026

Macdonald DW, Chapron G (2017) Outbreeding ideas for conservation success. Oryx 51: 206. https://doi.org/10.1017/S0030605317000151

Macdonald DW, Loveridge AJ, Dickman A, Johnson PJ, Jacobsen KS, Du Preez B (2017) Lions, trophy hunting and beyond: knowledge gaps and why they matter. Mammal Review: published online. [accessed: 31 July 2017]

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. Secretariat of the CBD, Montreal.

Panthera, WildAid, WildCRU (2017) Beyond Cecil: Africa's lions in crisis. Panthera, WildAid.

Ramsar Convention Secretariat (2010) Participatory skills: establishing and strengthening local communities' and indigenous people's participation in the management of wetlands. Ramsar Convention Secretariatm, Gland.

Ramsar Convention Secretariat (2013) The Ramsar Convention Manual. 6th ed. Ramsar Convention Secretariat, Gland.

Redpath S, Linnell JDC, Festa-Bianchet M, Boitani L, Bunnefeld N, Dickman A, Gutiérrez RJ, Irvine RJ, Johansson M, Majić A, McMahon BJ, Pooley S, Sandström C, Sjölander-Lindqvist A, Skogen K, Swenson JE, Trouwborst A, Young J, Milner-Gulland EJ (2017) Don't forget to look down – collaborative approaches to predator conservation. Biological Reviews: published online. [accessed: 24 March 2017]

Riggio J, Jacobson A, Dollar L, Bauer H, Becker M, Dickman A, Funston P, Groom R, Henschel P, De Iongh H, Lichtenfeld L, Pimm S (2013) The size of savannah Africa: a lion's (*Panthera leo*) view. Biodiversity and Conservation 22: 17–35. https://doi.org/10.1007/s10531-012-0381-4

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP, Schmitz OJ, Smith DW, Wallach AD, Wirsing AJ (2014) Status and ecological effects of the world's largest carnivores. Science 343: 1241484. https://doi.org/10.1126/science.1241484

Ripple WJ, Newsome TM, Wolf C, Dirzo R, Everatt KT, Galetti M, Hayward MW, Kerley GIH, Levi T, Lindsey PA, Macdonald DW, Malhi Y, Painter LE, Sandom CJ, Terborgh J, Van Valkenburgh B (2015) Collapse of the world's largest herbivores. Science Advances 1: e1400103. https://doi.org/10.1126/sciadv.1400103

Ripple WJ, Chapron G, Lopez-Bao JV, Durant SM, Macdonald DW, Lindsey PA, Bennett EL, Beschta RL, Bruskotter JT, Campos-Arceiz A, Corlett RT, Darimont CT, Dickman AJ, Dirzo R, Dublin HT, Estes JA, Everatt KT, Galetti M, Goswami VR, Hayward MW, Hedges S, Hoffmann M, Hunter LTB, Kerley GI, Letnic M, Levi T, Maisels F, Morrison

JC, Nelson MP, Newsome TM, Painter L, Pringle RM, Sandom CJ, Terborgh J, Treves A, Van Valkenburgh B, Vucetich JA, Wirsing AJ, Wallach AD, Wolf C, Woodroffe R, Young H, Zhang L (2016a) Saving the world's terrestrial megafauna. BioScience 66: 807–812. https://doi.org/10.1093/biosci/biw092

Ripple WJ, Abernethy K, Betts MG, Chapron G, Dirzo R, Galetti M, Levi T, Lindsey PA, Macdonald DW, Machovina B, Newsome TM, Peres CA, Wallach AD, Wolf C, Young H (2016b) Bushmeat hunting and extinction risk to the world's mammals. Royal Society Open Science 3: 160498. https://doi.org/10.1098/rsos.160498

Sandom CJ, Williams J, Burnham D, Dickman AJ, Hinks E, Macdonald EA, Macdonald DW (2017) Deconstructed cat communities: quantifying the threat to felids from prey defaunation. Diversity and Distributions 23: 667–679. https://doi.org/10.1111/ddi.12558

Scott KN (2016) Non-compliance procedures and the implemen tation of commitments under wildlife treaties. In: Bowman M, Davies P, Goodwin E (Eds) Research handbook on biodiversity and law. Edward Elgar, Cheltenham, 414–436. https://doi.org/10.4337/9781781004791.00025

Selier SAJ, Slotow R, Blackmore A, Trouwborst A (2016) The legal challenges of transboundary wildlife management at the population level: the case of a trilateral elephant population in Southern Africa. Journal of International Wildlife Law and Policy 19: 101–135. https://doi.org/10.1080/13880292.2016.1167460

TAWIRI (2007) Proceedings of the First Tanzania Lion and Leopard Conservation Action Plan Workshop. Tanzania Wildlife Research Institute, Arusha.

Treves A, Chapron G, López-Bao JV, Shoemaker C, Goeckner AR, Bruskotter JT (2017) Predators and the public trust. Biological Reviews 92: 248–270. https://doi.org/10.1111/brv.12227

Trouwborst A (2012) Transboundary wildlife conservation in a changing climate: adaptation of the Bonn Convention on Migratory Species and its daughter instruments to climate change. Diversity 4: 258–300. https://doi.org/10.3390/d4030258

Trouwborst A (2015a) Global large carnivore conservation and international law. Biodiversity and Conservation 24: 1567–1588. https://doi.org/10.1007/s10531-015-0894-8

Trouwborst A (2015b) Law and conservation conflicts. In: Redpath SM, Gutiérrez RJ, Wood KA, Young JC (Eds) Conflicts in conservation: navitaging towards solutions. Cambridge University Press, Cambridge, 108–118. https://doi.org/10.1017/CBO9781139084574.009

Trouwborst A (2017) Large carnivore conservation under the Bern Convention, with special reference to the Balkan lynx. Cat News: in press.

Trouwborst A, Krofel M, Linnell JDC (2015) Legal implications of range expansions in a terrestrial carnivore: the case of the golden jackal (*Canis aureus*) in Europe. Biodiversity and Conservation 24: 2593–2610. https://doi.org/10.1007/s10531-015-0948-y

Trouwborst A, Boitani L, Linnell JDC (2017a) Interpreting 'favourable conservation status' for large carnivores in Europe: how many are needed and how many are wanted? Biodiversity and Conservation 26: 37–61. https://doi.org/10.1007/s10531-016-1238-z

Trouwborst A, Fleurke FM, Linnell JDC (2017b) Norway's wolf policy and the Bern Convention on European Wildlife: avoiding the 'manifestly absurd'. Journal of International Wildlife Law and Policy 20: in press.

Trouwborst A, Blackmore A, Boitani L, Bowman M, Caddell R, Chapron G, Cliquet A, Couzens E, Epstein Y, Fernández-Galiano E, Fleurke F, Gardner R, Hunter L, Jacobsen K, Krofel M, Lewis M, López-Bao JV, Macdonald D, Redpath S, Wandesforde-Smith G, Linnell JDC (2017c) International wildlife law: understanding and enhancing its role in conservation. BioScience 67: published online. [8 August 2017] https://doi.org/10.1093/biosci/bix086

UNESCO, ICCROM, ICOMOS, IUCN (2012) World Heritage Resource Manual: Managing Natural World Heritage. UNESCO, Paris.

US Fish and Wildlife Service (2015) Endangered and Threatened Wildlife and Plants; Listing Two Lion Subspecies. Federal Register 80, 80000–80056.

Valeix M, Loveridge AJ, Davidson Z, Madzikanda H, Fritz H, Macdonald DW (2010) How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. Landscape Ecology 25: 337–351. https://doi.org/10.1007/s10980-009-9425-x

Venkataraman M, Macdonald DW, Montgomery R (2014) Managing success: Asiatic lion conservation, interface problems and people's perceptions in the Gir Protected Area. Biological Conservation 174: 120–126. https://doi.org/10.1016/j.biocon.2014.03.025

Wandesforde-Smith G (2016) Looking for law in all the wrong places? Dying elephants, evolving treaties and empty threats. Journal of International Wildlife Law and Policy 19: 365–381. https://doi.org/10.1080/13880292.2016.1248701

Watts S (2016) Protection of the African lion: a critical analysis of the current international legal regime. Potchefstroom Electronic Law Journal 19: 6. https://doi.org/10.17159/1727-3781/2016/v19i0a1158

Williams V, Newton D, Loveridge A, Macdonald D (2015) Bones of contention: an assessment of the South African trade in African lion *Panthera leo* bones and other body parts. TRAFFIC & WildCRU Joint Report.

Williams VL, Loveridge AJ, Newton DJ, Macdonald DW (submitted a) The trade in *Panthera leo* bones across Africa and to East-Southeast-Asia. Submitted to Plos ONE.

Williams VL, Loveridge AJ, Newton DJ, Macdonald DW (submitted b) Pan-African survey of the trade in lion body parts. Submitted to Plos ONE.

Wold C (2008) World Heritage Species: a new legal approach to conservation. Georgetown International Environmental Law Review 20: 337–396.

World Heritage Committee (2016) Operational Guidelines for the Implementation of the World Heritage Convention, update October 2016, WHC.16/01. UNESCO World Heritage Centre, Paris.

Wrangham RW, Hagel G, Leighton M, Marshall AJ, Waldau P, Nishida T (2008) The Great Ape World Heritage Species Project. In: Stoinski TS, Steklis HD, Mehlman PT (Eds) Conservation in the 21st century: gorillas as a case study. Springer, New York, 282–295.

Zhou Z, Newman C, Buesching CD, Meng X, Macdonald DW, Zhou Y (2016) Revised taxonomic binomials jeopardize protective wildlife legislation. Conservation Letters 9: 313–315. https://doi.org/10.1111/conl.12289

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When is it acceptable to kill a strictly protected carnivore? Exploring the legal constraints on wildlife management within Europe's Bern Convention

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Abstract

As wolf populations expand across Europe, many countries face challenges in finding ways to address the concerns of some elements among the rural stakeholders who are being asked to share their landscapes with wolves for the first time in several generations. In these recovery landscapes, wolves are associated with a wide range of conflicts that include economic, psychological, perceptional, social, cultural and political dimensions. A recurring demand concerns the desire to introduce the use of carefully regulated lethal control of wolves, through either culling by state employees or hunting conducted by rural hunters. Introducing such measures can be very controversial, and many critics challenge their legality under the international wildlife conservation instruments that have nurtured wolf recovery. We evaluate this issue for the case of wolves in Norway, which are strictly protected under the Bern Convention. Drawing on the latest results of social science research, we present the multiple lines of argumentation that are often used to justify killing wolves and relate these to the criteria for exceptions that exist under the Bern Convention. We conclude that while the Convention provides apparent scope for allowing the killing of wolves as a means to address conflicts, this must be clearly justified and proportional to the conservation status of wolves so as to not endanger their recovery.

Introduction

The last century has seen a dramatic recovery of large mammals in Europe. The first half of the 20th century saw the recovery of Europe's forests and large herbivores (Linnell and Zachos 2011) with large carnivores recovering in the latter half of the century (Chapron et al. 2014). This recovery was brought about by both active (reintroduction) and passive (fostering natural expansion) means; but builds on a fortunate coincidence of social, cultural, economic and ecological circumstances, and has been aided by wildlife conservation legislation at national and international levels (Linnell et al. 2009). Broadly speaking the task for the 21st century consists of learning to manage this success and ensure that the recovery is sustained (Swenson et al. 1998). Many ambitious visions of how far this recovery can continue are often articulated within the frames of the emerging rewilding discourse, for example. However, the growth of many conflicts (Redpath et al. 2013) associated with wildlife populations forces the consideration of the need to potentially limit recovery at levels below the biological potential (Boitani and Linnell 2015; Trouwborst et al. 2017a).

Many tools in the wildlife management toolkit can be used to foster a situation of coexistence rather than conflict (Carter and Linnell 2016). For example, there are a range of measures that can be adopted to protect crops and forests from herbivores and livestock from large carnivore attacks (Breitenmoser et al. 2005; Linnell et al. 2012), and many forms of structured dialogue exist to defuse social conflicts (Maser and Polio 2012; Reed 2008). Although these non-lethal methods may sometimes be challenging to implement they are usually not very controversial *per se*. In contrast, the use of lethal measures that involve killing wildlife can be highly controversial, from ecological, social, and legal points of view. This is especially true for large carnivores whose conservation is governed by various international legal instruments in addition to national and regional legislation.

In Europe, the most important pieces of international legislation are the 1979 Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats) administered by the Council of Europe, and the 1992 Habitats Directive (Council Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Fauna and Flora) administered by the European Union. All EU countries are subject to both instruments, whereas most European countries outside the European Union are subject to the Bern Convention only. International legislation is especially important in coordinating the conservation of highly mobile and low density species like large carnivores whose populations typically stretch across multiple countries (Trouwborst 2015a). It is widely recognized that international legislation such as these two instruments has been instrumental in fostering the recovery of large carnivores in Europe (Chapron et al. 2014; Fleurke and Trouwborst 2014). However, a key emerging question is to what extent international legislation provides constraints on the possibilities of individual countries adopting controversial measures such as lethal control.

In this article, we aim to provide background into the circumstances where lethal control has been claimed to offer potential utility and then explore the extent to which this can be permitted within the scope of the Bern Convention. We do not explore in depth the validity, or evidence base, behind the different claims as this would be far beyond the scope of a single paper. However, we do provide citations where they exist to relevant articles to document the plausibility of the claims. Our focus is the case of wolf (*Canis lupus*) management in Norway, which offers an extreme example of how a government seeks to use lethal control to severely limit population expansion to a bare minimum. However, this case study is directly relevant for parallel debates ongoing in other European countries, the United States, and other countries for wolves and other large carnivores, and we draw insights from parallel discourses and controversies for other species and countries.

This article is based on a range of methods, including; reviews of the available social science and ecological literature, multiple stakeholder dialogue processes at regional, national and European levels, twenty years of networking between researchers and wildlife managers across Europe and standard legal analysis methodology (Trouwborst 2015b). Most relevant are extensive stakeholder processes which were initiated in Norway in 2002-2003 (Andersen et al. 2004) along with 20 years of associated social science research. At the European scale, we draw on a series of stakeholder workshops organized for the European Commission between 2006 and 2014 in multiple countries across Europe (Linnell et al. 2008; Linnell 2013). Because the intention (teleology) of the law is a crucial part of any evaluation of areas that are not clear, we have included detailed discussions of ecological and social science aspects of wolf conflicts.

Europe's carnivores – recovery and conflicts

Historically, the populations of large carnivores in Europe were greatly reduced and even exterminated because of conflicts of interest with humans. Many of these conflicts have resurfaced as their populations expand, and have been joined by several new conflicts specific to our modern times. There has been intensive research from multiple disciplinary perspectives into these conflicts during the last 30 years to the extent that there is now a very good understanding of these issues (Redpath et al. 2013). The most important finding is that conflicts are diverse, occur along multiple dimensions, and can be highly variable across different contexts.

The most familiar conflict dimensions concern the direct economic and material impacts that large carnivores have on human property and activities. Depredation on livestock is a widespread problem for all large carnivore species (Kaczensky 1999). In addition, bears (*Ursus arctos*) are associated with damage to beehives, fruit trees and some agricultural crops (Bautista et al. 2017). However, recent research by the social sciences has also revealed the overriding importance of a set of conflict dimensions that do not directly concern economic losses (Linnell 2013; Redpath et al. 2013). Fear is a frequent component of conflict discourses. While the fear of bear attacks is easy to understand because the risks they represent are well understood (Penteriani et al. 2016), the fear of wolves has also emerged as a major discourse in areas where they return after long absences, despite the extremely low risk of actual attack (Røskaft et al. 2003; Linnell and Alleau 2015). A range of other social conflicts exist where large carnivores, especially wolves, have become symbols and surrogates for wider struggles such as those between traditional rural and urban publics, over modern vs traditional lifestyles and values, over different knowledge systems, and the struggle for power between regional, national and international bodies (Skogen et al. 2013). In other words, as well as conflicts between people and wolves there are conflicts between different groups of people about wolves, and especially about how they should be managed. However, it is also important to point out that many rural residents are positive about the presence of large carnivores, including wolves.

Based on considerable experience within networks of wildlife researchers and managers, we know that there is currently a broad understanding that sustaining large carnivores in the human dominated landscapes of modern day Europe requires a high degree of pragmatism and flexibility, especially when it comes to respecting the concerns of some segments of the rural publics whose lifestyles, livelihoods and well-being are the most directly affected. In many areas, this has led managers to allow some forms of lethal control and / or hunting of large carnivores. We explore the motivations for this in the next section, but first want to underline that well-regulated lethal control does not automatically represent a conflict with conservation goals. There is considerable experience within wildlife management institutions to manage hunting and control of large mammals, including large carnivores, through adaptive management frameworks where regular population monitoring is used to update quotas to minimize undesired developments in the size and distribution of the population (Linnell et al. 2010; Swenson et al. 1998). Our current biological understanding of these species also underlines that their interests are best served by fostering widespread and interconnected populations, and that this is more important than achieving locally high densities, especially when considering the long term need for gene flow (Linnell et al. 2008; Trouwborst et al. 2017a).

The multi-functionality of large carnivore hunting

In line with recent steps to recognize the multi-functionality of agriculture, there has been an increased recognition that hunting also serves multiple functions (Fischer et al. 2013). In the case of large carnivores there are at least seven lines of arguments that emerge from social science research and stakeholder engagement processes (Andersen et al. 2004; Bisi et al. 2007; Hiedanpää and Bromley 2011; Linnell 2013; Majic et al. 2011). We are not explicitly judging the objective validity of these arguments in this paper, but are rather trying to outline the arguments that are frequently raised by some rural stakeholders in favour of permitting the use of some form of lethal control and / or hunting of wolves. When it is considered how much focus is recently being placed on the need to manage perceptions of conflict as much as measurable and economic components of conflict (Redpath et al. 2013), there is clearly a need to give these arguments serious consideration. The overall relevance of these arguments is the claim that permitting lethal control and / or hunting will address some of the many conflicts associated with large carnivores. This is often summarized in the idea that being flexible on the means of conservation (i.e. not insisting on unconditional strict protection) will increase tolerance for larger populations of large carnivores spread over larger areas (Boitani and Linnell 2015). Our goal in this article is not to formally evaluate the validity of, or advocate, this argument. Rather we want to explore the extent to which the Bern Convention provides the flexibility to even consider such a strategy. In an earlier article (Trouwborst et al. 2017b) we have explored the issue of the level of conservation ambition (i.e. in terms of population *goals*) which the Bern Convention requires. In this article, we want to explore the issue of the *means* (i.e. when can lethal control be used) that are available to achieve these goals.

(1) **To reduce damage to livestock**. Lethal control or hunting can be used in many different ways to reduce damage to livestock. In some special cases where damage is caused by specific individuals it may be possible to selectively remove them, which may require very carefully targeted reaction or the use of "caught-in-the-act" mechanisms to kill specific individuals (Linnell et al. 1999). Translocation is no longer viewed as being a suitable non-lethal method for most situations (Linnell et al. 1997). Typically, above benefits cannot be achieved through a *de facto* hunting approach that tends to be conducted outside the grazing seasons and does not usually permit such careful targeting. However, hunting can also be used to lower the population density of carnivores in an area, which may lower depredation if depredation is density dependent (Herfindal et al. 2005; Tveraa et al. 2014; Mabille et al 2015), and it can be used to help prevent carnivore colonization of areas where local conflicts with livestock can be assumed to be inevitably high.

(2) **To maintain shyness**. The issue of individual wolves and bears not displaying the desired or expected level of shyness to humans has emerged as a key conflict area across Europe. While the phenomena associated with bears and food conditioning / habituation are relatively well understood from an ecological and management point of view (Huber et al. 2016), the parallel issue with wolves is not well documented (Linnell and Alleau 2015). The use of targeted control to remove specific individuals that display specific undesired behaviours is established as a fairly normal part of wildlife management practices, although it can still be controversial in certain cases (Rosen and Bath 2009). However, the utility of normal hunting to maintain shyness and prevent problematic behavior is not well documented, although it is widely claimed by hunters and rural residents to have such benefits (Cromsigt et al. 2013). Potential mechanisms include both behavioural learning through the disturbance associated with the process of hunting, and selection on different time scales by removing individuals with either learnt or inherited boldness (Borg et al. 2016; Starling et al. 2013).

(3) **Reducing competition for game with hunters.** Hunting wild ungulates for recreation, meat and trophies is widespread across most of Europe's surface, including within many protected areas. In addition, the hunting of wild ungulates helps provide benefits (economic and recreational) that offset some of the costs associated with their presence in human-dominated landscapes. There is widespread concern among hunters that the presence of large carnivores will lead to lower potential harvests and / or declines in prey (Andersen et al. 2006). Our current understanding of predator impacts on wild ungulates in Europe indicates that such impacts are likely to be highly context dependent, but where they are a potential issue the only way to alleviate them – bar-

ring a change in attitude and expectations by the hunters – is by maintaining carnivore populations at levels lower than their ecological carrying capacity. Another specific conflict with hunters in the Nordic countries concerns the tendency of wolves to kill hunting dogs (Butler et al. 2014). Although this phenomenon is not well understood, there is some evidence (Kojola et al. 2004), and widespread belief, that this behaviour is associated with specific wolf packs, which hunters then would like to see removed.

(4) **Empowerment**. The results of social science research indicate that many social conflicts are associated with rural communities that are asked to share their neighbourhoods and properties with large carnivores feeling a sense of disempowerment in the face of legislation imposed by distant external authorities (e.g. Hiedanpää 2013). Although dialogue processes and innovative management structures can provide some conflict reducing benefits concerning decision making, there are clearly limits to what can be achieved in such controversial conflicts (Hiedanpää and Bromley 2013; Madden and McQuinn 2014). There remains a frequently expressed desire from many rural people to be able to directly influence their own interactions with wolves using lethal control and / or hunting. This is often expressed in association with a desire to regulate the size and density of local populations, or at least to slow the rate of recovery to allow social / cultural adaptation to keep pace with the ecological changes (Carter and Linnell 2016; Kaltenborn and Brainerd 2016).

(5) **Normalisation**. In many parts of rural Europe sustainable hunting represents the "normal" form of human – wildlife relationship, for example with respect to other large mammals like deer and wild boar across most of the landscape. Norwegian laws (constitution, wildlife law, biodiversity law and animal welfare law) formally legitimise a philosophy that permits the sustainable use of natural resources, including wildlife, for economic, cultural and recreational purposes. A similar philosophy is also enshrined in the Convention on Biological Diversity which has a major influence on current European environmental law. Under such a regime, the act of killing wildlife is not viewed as being morally wrong in itself, although the process is subject to many restrictions related to ensuring sustainability and to animal welfare, public safety and property right considerations. This must be viewed in relation to a specific view of human – nature interactions which centers around ideas of active stewardship rather than passive protection (Kaltenborn et al. 2013a; Linnell et al. 2015). Therefore, when wildlife species like wolves receive strict protection it essentially conveys a different status on them, moving them from being "normal" and "natural" parts of the local fauna to being "the government's" animals and therefore less "natural". This alienation is associated with an opposition to accepting them and to accepting responsibility for adapting to their presence (Skogen et al. 2006). It is frequently suggested that allowing some form of hunting will "normalize" the presence of large carnivores, which is a crucial step towards building tolerance.

(6) **Adding value**. Permitting some form of *de facto* hunting creates the potential of attaching some value to the presence of large carnivores to help offset some of the costs. These values can be both in the form of economic values through the sale of trophy hunting licenses (Knott et al. 2014) and / or recreational values for rural residents (Kaltenborn et al. 2013a). This latter form of value can be seen in keeping with a way

of valuing wildlife based on relational values (sensu Chan et al. 2016) and a more traditional European view of nature conservation (Linnell et al. 2015). These economic and non-economic values can in principle help to raise the symbolic value of the wolf.

(7) **Reducing poaching**. The idea that illegal killing of wildlife will decrease as a result of allowing legal lethal control and / or hunting is widespread in the literature, although it is often posited without due consideration of the diverse motivations that underlie illegal killing (Chapron and Treves 2016), or the diversity of social and institutional contexts (Olson et al. 2015). For example, it is not only among poachers or potential poachers that management is seeking to gain tolerance as there are many other legal political pathways by which people can undermine conservation goals (Skogen and Krange 2003; Skogen et al. 2013). These nuances are highly likely to influence the logic underpinning the expected effect of legal harvest on illegal killing. However, in the case of Norwegian wolves it is not an unreasonable expectation that allowing legal harvest might prevent some of the illegal killing (indirectly supported by Kaltenborn and Brainerd 2016). While the outcome for the individual animal is the same (Vucetich et al. 2017), it has huge consequences for management as it permits greater precision in decision making as legal mortality is subject to regulation and monitoring, and poaching just induces stochasticity.

In summary, there are significant numbers of rural stakeholders which have raised multiple lines of argumentation in favour of allowing a relatively liberal use of exceptions to the strict protection status for wolves. These arguments involve the use of killing to manage both the economic conflicts and the perceptional / social conflicts associated with wolves. In effect, the arguments raised are based on the idea that allowing the killing of wolves, at levels that do not jeopardise their conservation status, will increase rural tolerance for the presence of wolves. As phrased here, the beneficial effect of allowing this killing will be enhanced if the killing is done by rural residents (rather than state agents) within a framework that approximates normal hunting as much as possible. A key aspect that has emerged in recent discussions about the pros and cons of lethal control concerns the need to demonstrate a utility of allowing control (Chapron and Treves 2016; Treves et al. 2016; Vucetich et al. 2017). These authors have focused on single or narrow dimensions of utility, which do not recognise most of the diverse aspects outlined above. Our point is that many traditional rural stakeholders identify multiple forms of utility, which are often based on a moral default position that does not assume that killing wildlife is wrong. Evaluating the support for these hypothetical relationships between killing and conflict goes beyond the scope of this article, although we hope this article will stimulate research on these issues. The question we do ask is whether this would be legal or not within the framework of the Bern Convention?

Large carnivores under the Bern Convention

Wolves are a typical example of a species for which international conventions like the Bern Convention where created as their populations span international borders and require cooperation between countries to achieve long term conservation gains (Trouwborst 2010, 2015). At the time that the Bern Convention was drafted in 1979, wolves where much less widespread in Europe than today, so it was logical that they were placed on Appendix II which conveys "strict protection", requiring a prohibition on *inter alia* the killing of any individuals (Article 6). Most of the countries that had large wolf populations at the time of ratifying the Convention submitted reservations exempting them from this designation, as permitted under Article 22 of the Convention (Salvatori and Linnell 2005). Lithuania and Spain opted to treat wolves as if they were on Appendix III, which generally permits sustainable exploitation but prohibits certain means of capture and killing (Articles 7 and 8), while other countries (Finland, Latvia, Belarus, Poland, Czech Republic, Slovakia, Ukraine, Bulgaria, and Macedonia) took a total reservation. The resulting legal landscape for wolves under the Convention is depicted in Figure 1. The expansion of wolves during recent decades has led to a situation where wolf population status has significantly improved in many areas, including in areas where they receive strict protection under Appendix II. In addition, some of the newer European countries and later contracting parties (e.g. Bosnia and Herzegovina, Montenegro, Albania, Romania, Croatia, Serbia, Estonia) with substantial wolf populations failed to file reservations regarding wolves upon ratifying the Convention. These two developments have led to varying degrees of actual or perceived mismatch between wolf population status within a country and its protection status under the Convention. Norway did not file a wolf reservation either, but wolves were (largely) absent from the country when it ratified the Bern Convention in 1986. At any rate, in Norway there is no mismatch between the strict protection status under the Convention and their currently minimal wolf population. Similar considerations apply to Switzerland.

A note on interpreting the Convention and its relationship with the EU Habitats Directive

Article 9 of the Bern Convention states various criteria that need to be met before exceptions from strict protection can be made. The article should be read in light of the general rules governing treaty interpretation. According to the 1969 Vienna Convention on the Law of Treaties (VCLT) and customary international law, a treaty should be interpreted "in good faith in accordance with the ordinary meaning to be given to the terms of the treaty in their context and in the light of its object and purpose" (Vienna Convention, Article 31.1). In addition to treaty text and objectives, "any subsequent agreement between the parties regarding the interpretation of the treaty or the application of its provisions", "any subsequent practice in the application of the treaty which establishes the agreement of the parties regarding its interpretation", and "any relevant rules of international law applicable" may be taken into account (Vienna Convention, Article 31.3). Finally, the original intentions of the parties, as recorded in the treaty's drafting history, can be considered as a supplementary means if necessary. In the case of the Bern Convention, an "Explanatory Report" records some of the intentions of the *ad hoc* Committee that drafted the Convention text. Whereas

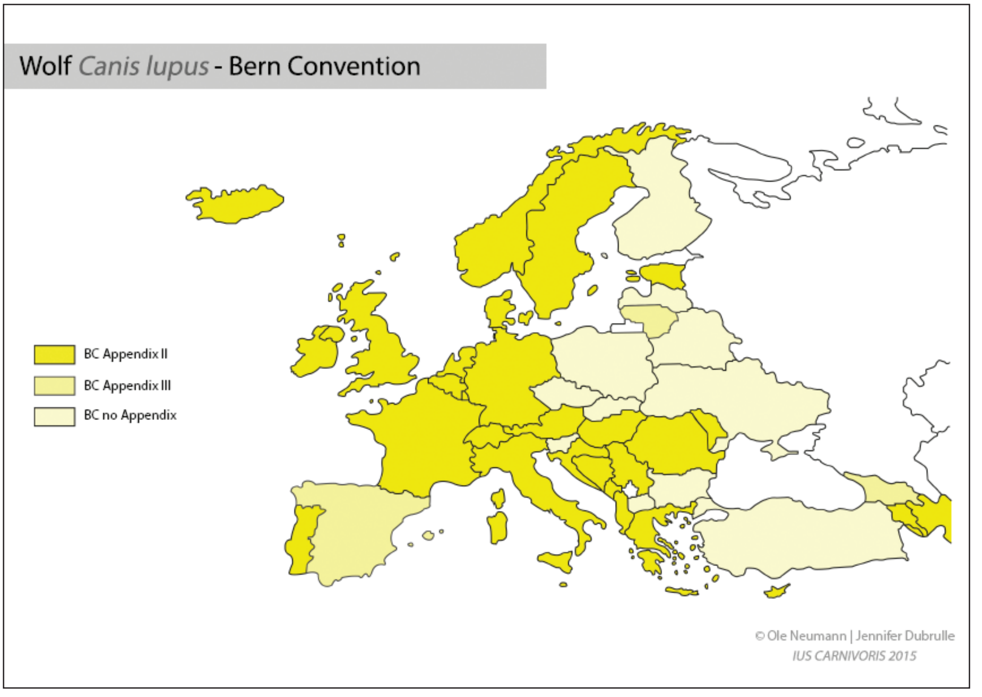

Figure 1. The legal status of wolves under the Bern Convention.

the Report itself notes that it "may facilitate the understanding of the Convention's provisions," the Report "does not constitute an instrument providing an authoritative interpretation of the text of the Convention" (Explanatory Report, para. II). Of special relevance for our present purposes is Revised Resolution No. 2 (1993), adopted in 2011 by the Standing Committee of the Bern Convention (the Convention's main decision-making body in which all parties are represented) in order to "further clarify the conditions laid down in Article 9 for the granting of exceptions." The Resolution has an Appendix entitled "Interpretation of Articles 8 and 9 of the Bern Convention" [hereinafter "Appendix to Resolution No. 2"]. In the Resolution itself, the Standing Committee "recommends that Contracting Parties bring the appended document, which contains useful guidance for interpreting the scope of Article 9, to the attention of all those responsible for applying and interpreting the Convention in their respective countries". Within the scheme of the VCLT, the guidance provided in the Appendix thus appears to have significant interpretive value in terms of "subsequent agreement". We also draw attention to the legal analysis prepared by a consultant in connection with the development of Revised Resolution No. 2, which is a helpful background document (Shine 2010).

The case law of the Court of Justice of the EU (CJEU) and the European Commission's guidance regarding the application of derogations from strict protection under Article 16 of the Habitats Directive – the counterpart (and implementation) of Article 9 of the Bern Convention – is instructive too. Even if this case law and guidance do not apply to non-EU member states like Norway, they do represent an approach that could *prima facie* be presumed to be consistent with the Bern Convention as the EU and its member states are parties to the Convention, and the Habitats Directive is expressly intended to implement the Convention within the EU (Epstein 2014). Furthermore, the vast majority of wolves within the Scandinavian population are within an EU member state, Sweden, such that it is important to understand practices in all parts of the population in order to assess cumulative effects. We will therefore make some reference to case law and guidance regarding the Habitats Directive.

However, it is important to apply restraint in the degree to which such case law and guidance under the Habitats Directive is considered indicative of the correct interpretation of the Bern Convention. This is so for the plain reason that the Bern Convention is the leading framework, higher up in the hierarchy than the Habitats Directive. Thus, the Directive must conform to the Convention, not the other way around. This effectively precludes the Directive's regime from providing EU member states with broader possibilities for killing strictly protected Bern Convention species than the Convention itself provides. Conversely, it *is* possible for the Directive to be more restrictive in this regard, and indeed Article 12 of the Convention expressly allows this. However, to what extent the Directive in fact imposes further constraints on national authorities for the killing of wolves and similar species than the Convention does is not a question we aspire to answer in this article (but see, e.g., Darpö and Epstein 2017).

Does the Bern Convention seek to conserve wildlife populations or to protect individual animals from being killed?

There are many different visions of nature conservation (Linnell et al. 2015; Mace 2014). A fundamental aspect of our discussion concerns determining if the Bern Convention seeks to conserve wildlife populations using protection as a context-dependent tool, or if the protection of individuals from anthropogenic mortality is an explicit objective in itself. Our view is that the Convention definitely reflects the former approach, i.e. aiming at the conservation of populations, based on the following lines of evidence.

(1) Throughout the preamble and Articles 1-3 the Convention's text uses the word "conservation" to refer to goals. Explicitly, Article 2 refers to "…maintain the population of wild flora and fauna …".

(2) The fact that there are two different appendices for wildlife species, where Appendix III opens for exploitation, implies that the prevention of killing that is required for Appendix II species is a context-dependent measure appropriate for some species in some countries and necessary for their conservation, rather than an independent objective.

(3) The Convention applies to the entire European landscape, not just protected areas, which implies a recognition of the multi-use landscape in which European wildlife conservation occurs. This, in turn, automatically implies the need for pragmatic management and compromises, which is explicitly recognized in Article 2's text that

allows populations to be “adapted” to other considerations than ecological ones, and in the inclusion of Article 9 that opens for exceptions from Appendix II’s prohibition on killing. The Bern Convention was apparently intended by its drafters as “an instrument that would permit flexibility of action within a common purpose” (Explanatory Report, para. 10), and the possibility of derogations from strict protection in Article 9 clearly reflects this approach.

(4) The word “protection” is not used as an opposite to killing (as in the widespread modern sense of the meaning of the word protection). For example, Article 7 requires parties to “… ensure the protection of the wild fauna species ….” but then goes on to permit the “…. exploitation of wild fauna ….”. It is important to remember that the Convention was written in the 1970s before much of the present-day terminology of sustainable use, conservation biology, biodiversity and animal welfare had developed. In this period “protection” referred to the inclusion of wildlife within a legal framework that limited human actions because the default at the time was a lack of any legal status at all. In other words, protection referred to “inclusion in a legal framework” rather than “protect all individuals from deliberate killing”.

(5) Animal welfare considerations are implicitly included via Appendix IV’s listing of prohibited mechanisms of killing.

(6) Article 2 formulates the goals of the Convention and recognizes that the conservation goals for a species need to take into account a diversity of interests, including cultural, economic and recreational requirements, in addition to the ecological. This can be taken as explicit recognition of the need to find compromises between competing interests, even if Article 2 must clearly be interpreted as giving precedence to ecological considerations in cases of irreducible conflict (Trouwborst et al. 2017b). Two of the most relevant interests that potentially compete with the Convention’s primary ecological imperative are hunting and livestock grazing. Hunting of wild ungulates is clearly a major source of income, cultural tradition and recreational value in rural Norway, as in most of Europe. Livestock grazing is also widespread and serves as both an economic activity in rural areas, and as a potentially important action required to maintain grazing dependent biodiversity and cultural landscapes (highlighted in the 2000 European Landscape Convention, for example). The semi-domestic reindeer herding conducted by the indigenous Sami people of central and northern Fennoscandia is clearly an important cultural activity, which is also protected by other conventions such as the 1989 Convention concerning Indigenous and Tribal Peoples in Independent Countries (ILO Convention No. 169), the Norwegian Nature Diversity Act of 2009 (section 1) and the Norwegian constitution (§ 108).

In summary, the Convention’s objectives are evidently focused on the conservation of populations, whereby strict protection of individual animals is one means that may be needed to achieve this goal within certain contexts. However, it is important to underline that none of these arguments permit deviation from the obligation to work towards and ultimately ensure a population level conforming to the requirements of Article 2 of the Convention.

The role of cultural requirements within the scheme of the Convention

Building on our prior analysis of Article 2 (Trouwborst et al. 2017b), it is appropriate in the present context to dwell on the reference this provision makes to "cultural requirements". In particular, Article 2 obliges Bern Convention parties to "take requisite measures to maintain the population of wild flora and fauna at, or adapt it to, a level which corresponds in particular to ecological, scientific and cultural requirements, while taking account of economic and recreational requirements and the needs of sub-species, varieties or forms at risk locally." The reference to cultural requirements is somewhat enigmatic. As Bowman et al. (2010: 300) note, "it would certainly be difficult to [define a population level] by reference to cultural considerations." However, the insertion of the word "cultural" must have happened for a reason, and it seems reasonable to assume, therefore, that cultural requirements such as preservation of local ways of (human) life could exert an influence on the population level required by Article 2, both upwards and downwards, depending on the circumstances. Nevertheless, it would *not* be reasonable to assume that cultural considerations could justify a population level that is so low that the population is actually threatened. In other words, ecological requirements would appear to impose an absolute minimum, the breaching of which cannot be justified by cultural requirements or otherwise. Where precisely *above* this absolute minimum parties should aim the population level to be, would appear to be the result of a balancing of ecological, scientific and cultural requirements, and to a lesser extent economic and recreational requirements as well.

The existence of the aforementioned minimum population level – where ecological requirements would trump cultural requirements besides economic and recreational ones (Bowman et al. 2010; Trouwborst et al. 2017b) in case of conflict – follows *inter alia* from the Convention's objective as formulated in Article 1, which makes clear that the *exclusive* aim of the Convention is wildlife conservation, not conservation of human cultures or economies. That Article 2 should logically be interpreted in light of this objective as formulated in Article 1 is further reinforced by the Explanatory Report to the Convention, which succinctly states (in para. 21) that Article 2 "contains a main obligation that follows from the aims stated in Article 1, paragraph 1." An interpretation whereby cultural requirements would be presented as justifying a population level at which the population is actually threatened is thus simply untenable in light of the basic rules of treaty interpretation. The separate minimum requirements of the "survival of the population" set out in Article 9 and keeping "populations out of danger" set out in Article 7 would also independently prevent "cultural requirements" from justifying policy targets set at a level where the population would be threatened.

As we acknowledged earlier (Trouwborst et al. 2017b), where the aforementioned absolute minimum population level required by Article 2 lies precisely is difficult to pinpoint. There are, however, certain indicators of potential utility. In Norway, for instance, once wolves are no longer listed as threatened on the national Red List, that would appear to provide the authorities with an argument to say that the population of wolves in Norway corresponds to ecological requirements as demanded by Article 2. The same could probably be said if wolves in Norway can be shown to be at a "favourable conservation status" as defined under the Habitats Directive.

Exploring the legality of lethal control

Article 9 of the Bern Convention outlines the conditions under which exceptions from the provisions of Articles 4, 5, 6, 7 and 8 can be granted. (It should be noted that exceptions may *not* be made to the general obligation in Article 2 to secure a particular population level for all wildlife.) Article 9 sets two preconditions before any exception to the prohibition on killing strictly protected wolves can be granted. These are "that there is no other satisfactory solution" and "that the exception will not be detrimental to the survival of the population concerned". If these preconditions are met there are five reasons identified that may justify an exception, four of which are relevant for our discussion. These are:

9.1.i - "for the protection of flora and fauna",

9.1.ii - "to prevent serious damage to crops, livestock, forests, fisheries, water and other forms of property",

9.1.iii - "in the interests of public health and safety, air safety or other overriding public interests",

9.1.iv - "for the purposes of research and education, of repopulation, of reintroduction and for the necessary breeding",

9.1.v - "to permit, under strictly supervised conditions, on a selective basis and to a limited extent, the taking, keeping or other judicious exploitation of certain wild animals and plants in small numbers".

An important question concerns the burden of proof. The general assumption here is that the contracting party involved must be able to adequately justify the exceptions it allows or makes by demonstrating that all three conditions of Article 9 are met. As one Bern Convention guidance document (T-PVS/Inf (2010) 16) puts it: "Competent authorities need to explain the particular circumstances justifying the choice of an Article 9.1 reason and verify that the specific conditions are met." There is currently a general lack of documentation about the utility of many lethal and non-lethal approaches to interventions aimed at the relatively simple conflict associated with livestock depredation (Eklund et al. 2017; Treves et al. 2016), let alone the more complex social/cultural conflicts (Reed 2008; Sandström et al. 2009). However, providing evidence that allowing more liberal killing of wolves helps to increase tolerance requires that it is actually tested and evaluated, so there can be a catch-22 situation where proof is needed, but cannot be obtained until tested.

Condition #1: No satisfactory alternatives

Regarding the condition that derogations may only be authorized when "there is no other satisfactory solution", the Appendix to Resolution No. 2 holds that the authorities should "choose, among possible alternatives, the most appropriate one that will have the least adverse effects on the species while solving the problem," while adding that the reasoning backing the choice made should be "objective and verifiable". Regarding the prevention of damage to livestock or other property, "less oppressive measures" can be considered as an alternative solution to killing.

When discussing the satisfactory alternatives test, the European Commission's guidance regarding the Habitats Directive emphasizes that "recourse to Article 16 derogations must be a last resort" (European Commission 2007, para. 38, emphasis in original). It is furthermore observed that:

"The appraisal of whether an alternative is satisfactory or not, in a given situation, must be founded on objectively verifiable factors, such as scientific and technical considerations. In addition, the solution finally selected, even if it involves a derogation, must be objectively limited to the extent necessary to resolve the specific problem or situation. Evidently, the requirement to consider seriously other alternatives is of primary importance. The discretionary power of Member States is limited, and where another solution exists, any arguments that it is not 'satisfactory' will need to be convincing. Moreover, it should be stressed that another solution cannot be deemed unsatisfactory merely because it would cause greater inconvenience to or compel a change in behavior by the beneficiaries of the derogation." (European Commission 2007, paras. 40-41)

The assessment whether there exists any "other satisfactory solution" should be context-dependent and involve a confrontation of the measure reviewed (e.g. hunting) with the alternative measures so as to be certain that the restrictions imposed are justified. This amounts to a proportionality test: a) is the alternative effective, and b) can the alternative achieve the same end in a way that is less harmful to the carnivore's population?

There is considerable experience across Europe when it concerns protecting domestic livestock from large carnivore depredation (Breitenmoser et al. 2005; Linnell et al. 2012). A range of measures including electric fencing and intensive shepherding, both of which can also involve livestock guarding dogs, exist that can greatly reduce losses. However, the introduction of these measures can be very expensive and be associated with logistical challenges, certainly under Norwegian conditions (poor quality of grazing pastures, land-ownership patterns, high labour costs, and restrictive labour laws). The question then arises to what extent it is expected that Norway adapt a nationwide practice to accommodate wolves or how quickly this transition should occur? Norwegian wolf policy documents have been evolving since the 1980s. Throughout the late 1980s and 1990s it was already clear to policy makers that the areas along the border with Sweden would be the most likely to house a future wolf population (this was formally designated as a "wolf zone" in 2001) and also that dramatic changes to livestock husbandry would be needed (Miljøverndepartementet 1992, 1997, 2003).

Therefore, there has been over 30 years of awareness of the issue in the area within and surrounding the current wolf zone. For semi-domestic reindeer, the situation is somewhat different as there are virtually no practical protective measures that can be adopted to hinder serious depredation by wolves, although compensation does exist to mitigate the economic losses.

In contrast, there is much less experience when it comes to demonstrating what works and what does not work to reduce social and perceptional conflicts. There is considerable practical experience with stakeholder processes (Reed 2008) and various forms of inclusive management in Europe (Sandström et al. 2009; Redpath et al. 2017). However, although inclusive management may be intrinsically important to satisfy modern day democratic principles and to address a sense of justice (Jacobsen and Linnell 2016) it is unclear if it alone can diffuse such complex conflicts as those associated with large carnivores. Information is often touted as a solution to some social conflicts, but again there are doubts concerning the extent to which it alone can address these wolf conflicts (Ericsson and Heberlein 2003). When considering how any measures might be successful in diffusing these conflicts it is crucial to consider how a package of multiple measures will come to bear on multiple conflict dimensions. This makes the task of documenting effects challenging, an issue made worse by the long memory of many of the parties in the conflict, such that any new measures will still be interpreted in light of perceived shortcomings of previous strategies. In conclusion, it will be highly challenging to document, or reject, the utility of any single measure used to address social and perceptional conflicts.

Condition #2: No detrimental effect on the population

With regard to the condition in Article 9 that a derogation must not be "detrimental to the survival of the population concerned," according to the Appendix to Resolution No. 2 the assessment whether this is so "should be based on current data on the state of the population, including its size, distribution [and] future prospects." It is also made clear that account must be taken of "cumulative effects of several derogations," and that "special caution should be taken in case of species that are not in 'favourable' conservation status." There are four issues here relevant for the current discussion. The first concerns the number of animals to be killed relative to the size of the population. The smaller the proportion of the population to be killed, the more likely it is to be legally acceptable. Secondly, the implications of this depend very much on the scale of assessment, i.e. if we view the population as the wolves present in Norway, those present in Scandinavia, or those present in Fennoscandia and western Russia. The key biological issue here is that killing individuals in a small unit will always have greater uncertainties attached to it than the same actions in large units because the role of chance events is automatically greater in small units. Thirdly, there is a need to consider all mortality within the unit of assessment. If the assessment refers to the Scandinavian population, then it would imply a need for a formal coordination of planned mortality in both Norway and Sweden. No such coordination exists. Furthermore, the

Bern Convention's Standing Committee has recommended a set of guidelines on population level management of large carnivores (Linnell et al. 2008) to parties (Recommendation No. 137 (2008)) where a central tenet is that the use of the transboundary population level as the benchmark for assessments in connection with Article 9 should only be considered when formal management plans exist at the transboundary population level (Trouwborst et al. 2017a and 2017b). Finally, irrespective of the scale of assessments, all parties to the Convention have individual responsibilities towards species conservation and cannot outsource these to other countries (Trouwborst et al. 2017b). In the current Norwegian context with its small population, the condition of no detrimental effect is evidently a high hurdle.

Serious damage

Insofar as the purpose of a derogation is "to prevent serious damage", the interpretive guidance in the Appendix to Resolution No. 2 provides the following:

"If 'damage' is taken to mean prejudice sustained by a person as a result of damage caused to those items of property that are listed in Article 9, paragraph 1, second subparagraph, and it seems legitimate to do so, then the adjective 'serious' must be evaluated in terms of the intensity and duration of the prejudicial action, the direct or indirect links between that action and the results, and the scale of the destruction or deterioration committed. 'Serious' does not, of course, necessarily mean that the damage was widespread: in some cases the item of property affected may cover only a limited geographical area (for example, a region), or even a particular farm or group of farms. However, the exceptions should be proportional to the damage suffered: the fact that an isolated farm sustains damage would not appear to justify the capture or killing of a species over a very wide area, unless there is evidence that the damage could extend to other areas. It is not required that the damage be already present. Rather, it is sufficient if serious damage in all likelihood will occur."

The exception is limited to property, which in a Norwegian context would automatically include livestock, semi-domestic reindeer, dogs, beehives etc. The extent to which it can be extended to game populations has frequently been raised in policy debates and there is still some perceived uncertainty, as it depends if one refers to the game itself (not property) or the hunting rights (linked to property rights).

Overriding public interest

Regarding the meaning of the term "overriding public interest", it would seem on the one hand that the Norwegian authorities have quite some discretion to determine themselves what they consider the term to cover. As Bowman et al. (2010: 318) put it, "the phrase 'other overriding public interests' appears to give the parties a disturbingly wide margin of discretion." On the other hand, invoking this clause is certainly not a purely *pro forma* matter either, and indeed the Appendix to Resolution No. 2 considers the interpretation of the words "overriding public interest" to constitute "a very difficult problem". Norway would be expected, when invoking it, to muster an adequate measure of concrete justification of the "public" and "overriding" nature of the issue. The latter term requires argumentation that the conflict reduction interest in which wolves are to be culled "overrides" the conservation utility of upholding the prohibition on killing them – a determination to be made in good faith and in light of the Bern Convention's objectives. The Appendix to Resolution No. 2 takes the position that if push comes to shove it is up to the Standing Committee to determine whether an interest advanced by a certain party as an "overriding public interest" must indeed be considered to qualify as such, and that "in the event of difficulties" (i.e., disagreement between parties in this regard), the matter could be referred under Article 18 to an arbitral tribunal for definitive settlement. In light of the above, it would seem that protecting the aforementioned rural interests could in theory be construed as a matter of "overriding public interest" – especially in light of the fact that Norway has an active rural policy enshrined in policy and legislation. However, any explanation furnished by the Norwegian authorities must be persuasive. Whether killing wolves is then the best or only viable means to serve such supposed overriding rural interests will be the subject of the alternatives test discussed above.

Public safety

The Explanatory Report clarifies that killing individual large carnivores should not be problematic in situations where public safety is at real and imminent risk. The Explanatory Report, para. 39 states that "there might be emergency cases where exceptions would have to be made without all conditions [of Article 9] having been fulfilled (e.g. the abatement of rabies)". Furthermore, paragraph 31 states that the prohibitions of Article 6(a)-(c) do not apply in situations of self-defence: "It was not thought necessary to specify explicitly that the provisions under a, b and c would not apply in case of self-defence".

Judicious use

Regarding the 'judicious use' clause from Article 9 ("to permit, under strictly supervised conditions, [etc]"), the accompanying conditions are procedural rather than substantive in the sense that, as the Appendix to Resolution No. 2 states, this ground may be invoked by a contracting party "for any reason which to it seems valid (for instance, hunting, recreation, etc)," although the party should "ensure that such reason is clearly identified." The Appendix also states that a derogation based on the judicious use clause "should be temporary but may be renewed from time to time." Generally, the scope this clause offers for justifying wolf culling appears to be tightly related to the overall number of wolves in Norway, as the overall status and trend of the wolf population would heavily influence the interpretation of what is "judicious" and what are "small numbers". As the Appendix to Resolution No. 2 puts it, "the expression 'small numbers' should thus be construed in the light of the state of the conservation of the population." To illustrate, killing 20 out of a total of 60 wolves would hardly qualify as "small numbers", but killing the same 20 wolves out of a total population of 2000 wolves may very well do. Thus, in Norway, the current small wolf population and minimalist population target would seem to preclude a meaningful role for the judicious use clause in the foreseeable future.

It should be noted, moreover, that according to the interpretive guidance in the Appendix to Resolution No. 2, the wording "under strictly supervised conditions" should be understood to mean that "the authority granting the exception must possess the necessary means for checking on such exceptions either beforehand (e.g., a system of individual authorisations) or afterwards (e.g., effective on-the-spot supervision), or also combining the two possibilities." In addition, the expression "to a limited extent" suggests, again in the words of the Appendix, that the authorized measures should be "limited in both space and time."

Norway, together with Sweden, has invested in what are probably the world's most intensive monitoring programs for large carnivores (http://www.rovdata.no). When it concerns wolves, this includes annual counts of numbers of packs and reproductions, an overview of the location of non-breeding, but territorial, pairs, and an assessment of genetic identity that for most individuals extends to knowledge of their full pedigree and inbreeding coefficients (e.g. Bensch et al. 2006). Effective wildlife management institutions are in place to set and monitor quotas as well as regulate the number of hunters allowed to engage in lethal control and hunting. Although the meaning of "selective basis" seems to mainly apply to ensuring that only the right species is killed (Shine 2010), the management institutions in place have no problem in focusing the killing of wolves on specific packs and regions. There are no obvious reasons why this form of controlled hunting could not be done by rural hunters as opposed to state agents, and indeed most of the proposed benefits of hunting will only be achieved by allowing rural hunters to conduct the activity.

Interestingly, Norway did not include this judicious use clause (Bern Article 9.1.v) in its 2009 Nature Diversity Act which otherwise included the other clauses. An attempt to modify the Nature Diversity Act accordingly in spring 2017 failed. However, our discussion of this clause is still important in case of future changes to the law, and for the more general value of this discussion for other Bern Convention countries.

Ending suffering

According to the Explanatory Report, para. 39: "It was considered that the taking or killing of protected fauna for humane or humanitarian reasons was an accepted practice that did not require a specific provision in the Convention." This would presumably apply to a wolf badly injured through accidental collision with a vehicle, for example. This is also supported by paragraph 4 "Duty to help" of Norway's Animal Welfare Act of 2009.

Guidance from the Habitats Directive

Substantively, the Habitats Directive has copied the structure of the Bern Convention. In both instruments the wolf is listed as a strictly protected species and is protected in a similar way (although many countries also registered exceptions for wolves). As in the Bern Convention, the system of strict protection must include the prohibition of the "deliberate capture or killing of these species" (Habitats Directive, Article 12). Also comparable to the Convention, exceptions to this strict protection regime may be justified when one of the five grounds occurs, when there is "no satisfactory alternative", and such an exception would not be detrimental to the maintenance of the populations of the species concerned at a favorable conservation status in their natural range (Article 16.1).

The 2007 Finnish wolf case, in which the CJEU ruled on the compatibility of lethal control of wolves with their conservation, could be helpful when interpreting Norway's obligations under article 9 of the Bern Convention. The case concerned 22 Finnish hunting permits that allowed the killing of individual wolves in order to prevent serious damage to livestock and dogs. This ground for derogation is listed under article 16.1 of the Habitats Directive, and mirrors one of the grounds for derogation under the Bern Convention. The Commission brought an infraction action against Finland claiming that since (i) the conservation status of the wolf was not favourable in Finland, (ii) alternative approaches could be employed and (iii) hunting permits were issued without establishing that these particular wolves caused serious damage, the authorization to hunt wolves did not satisfy the conditions laid down in Article 16.1 of the Habitats Directive (Case C-342/05, Commission v Finland).

The Court reiterated that the favourable conservation status of the populations of the species concerned in their natural range is a necessary precondition for the derogations to be granted. Nevertheless, it held that the granting of such derogations remains possible by way of exception if they do not worsen the unfavourable conservation status of those populations or prevent their restoration at a favourable conservation status. Thus, if the killing of a limited number of wolves has no effect on the objective of maintaining the population at a favourable conservation status in its natural range, such killing may be allowed. In any event, such a decision has to be aimed at animals likely to cause damage, be based on an assessment of the effect of the killing on the maintenance at a favourable conservation status of the population, and should contain a clear and sufficient statement of reasons as to the absence of a satisfactory alternative.

Regarding the complaint by the Commission that hunting permits were issued on a preventive basis or without any relationship with the particular wolves causing serious damage the CJEU observed that Article 16.1 of the Habitats Directive does not require serious damage to be sustained before derogating measures can be adopted. The Court, however, did not define what constitutes "serious damage" or to what extent wolf culling on a preventive basis is allowed (e.g. to improve social tolerance for species), but it did point out that there was little biological research available on the question of whether continued hunting keeps wolves wary of humans and thus helps to reduce damage. It concluded therefore that "in those circumstances, the Commission's complaint relating to the fact that hunting permits are issued on a preventive basis must be upheld" (Case C-342/05). As the Court concluded, by authorising wolf hunting on a preventive basis, without it being established that the hunting is such as to prevent serious damage, Finland has failed to fulfill its obligations under the Directive (Epstein 2017).

Conclusions

The Convention's objectives

The sole overarching objective of the Bern Convention is nature conservation. The arena for conservation in which the Bern Convention was crafted to operate, however, is the entire multi-use and human-dominated of landscape of Europe, not just the protected areas. Besides ecological requirements, the Convention therefore also caters for the incorporation of economic and cultural requirements. As long as the paramount minimum requirements regarding species' conservation status are met, the Convention provides room for flexibility, exceptions, and necessary management actions.

Furthermore, our analysis confirms that the Bern Convention is intended to promote the conservation of wildlife populations rather than prevent the killing of individual animals *as such*. Avoiding the deliberate killing of animals was included as a context dependent measure to bring about these goals when needed. A problem is that there is an apparent lack of consistency concerning which countries opted for reservations for Appendix II designation of wolves and the present status of their wolf populations. Furthermore, the existing mechanism (Article 17) to permit the adjustment of Appendix designation in response to the success or failure of conservation measures over time has not been utilised very often, and the dozen occasions on which the appendices have been amended all involved the addition of new species. Considering that more than 37 years have passed since the Convention was drafted and the appendices drawn up it is not surprising that there are now some questions about the extent to which they match the conservation status of certain species on the ground, particularly where conservation status has markedly improved. It should be noted that this issue clearly does not apply to Norway and its critically endangered wolf population.

Proportionality

In our view, the Convention provides for many options that allow for the killing of wolves (and other strictly protected species) for multiple legitimate reasons (Box 1). These can be interpreted as covering issues related to protecting property (like livestock), protecting human safety, and responding to a wide range of the other social conflicts associated with wolves. However, none of these allow deviation from the ob-

Box 1. Evaluating different situations.

Based on our exploration of the potential motivations to deviate from the prohibition on "deliberate killing" for Appendix II species there are five broad scenarios under which exceptions are likely to be sought. Here we try to summarise to what extent they are likely to be acceptable in terms of one (or more) of the reasons for derogating from strict protection mentioned in Article 9.1 of the Bern Convention. The codes in parentheses refer to the clauses in Article 9.1, in decreasing order of applicability. It is important to note that in all cases there is also a need to verify and document that no satisfactory alternatives exist, that the cumulative exceptions will not jeopardise the population (Article 9), and that the overall conservation obligation (outlined in Article 2) is met.

Scenario 1: Humanely ending the life of a large carnivore suffering from injury or disease from which it cannot recover.

- Should be unproblematic (Explanatory Report).

Scenario 2: Responding to a specific individual carnivore's damage to property, such as livestock or beehives.

- Should be unproblematic if a specific problem individual or pack can be identified *and* if the level of damage is serious *and* if best practice protective measures have been adequately utilized but proven ineffective (because no alternative livestock protection measures provide 100% protection, as some individual carnivores inevitably find a way past them) (Article 9.1.ii).

Scenario 3: Responding to a specific individual carnivore's potentially dangerous behavior with respect to humans.

- Should be unproblematic if an individual (or social group) has attacked people, or has shown unquestionably threatening behavior, or has a dangerous disease such as rabies (Explanatory Report and Article 9.1.iii).
- The challenge is to identify objective criteria to assess the potential risk from different behaviours in the absence of direct attacks or unambiguous threats. The knowledge of risk factors associated with wolf behavior lags far behind that for bears, requiring the development of guidelines based on best available knowledge. A second requirement is to effectively link allowing killing of individuals to the reduction of risk.

Scenario 4: Lethal control to limit a population's growth and distribution, or slow its growth rate so as to permit time for human adaptation (i.e., gradual adoption of alternative measures).

- Easier to argue for semi-domestic reindeer than for sheep because suitable alternatives exist for sheep, but not for reindeer, and the cultural aspects of reindeer herding are more easily identified within legal frames. For sheep husbandry, the question concerns over how wide an area, and how quickly, these alternative forms of husbandry should be introduced. (Article 9.1.ii, 9.1.iii). This is also linked to the discussion of the level of ambition of conservation goals (Trouwborst et al. 2017b).
- Can potentially be used to limit predator impact on wild game of importance to hunters (Article 9.1.ii, 9.1.iii) if hunting is identified as an issue of overriding public interest or if game harvesting is included as a form of property right.

Scenario 5: Permit a sustainable harvest of a population to reduce social conflicts and promote tolerance among rural residents.

- Not automatically acceptable, but could potentially be argued in relation to a broad set of arguments linked to maintaining rural lifestyle and addressing social conflicts such as empowerment or recognition of multiple values, as well as economic issues where losses occur. This would be especially true if it can be shown that conflicts are related to carnivore population density which is certainly probable for conflicts with hunting interests and with livestock in some cases (Article 9.1.v, 9.1.iii, 9.1.ii, 9.1.i).

ligation to make a real commitment to the conservation of the species in question by ensuring a population level that "corresponds to [*inter alia*] ecological requirements," as demanded by Article 2 of the Convention (Trouwborst et al. 2015a, 2017b). Also, the requirement that alternatives to killing be identified – and, where available, used instead of killing – is paramount, as is the need to ensure that the cumulative effect of all actions does not jeopardize the survival of the population.

There is also the clear need for a degree of proportionality. The numbers being killed, and the threshold below which animals cannot be killed must be seen in relation to both the degree of conflict and the size of the population. It would therefore be easier for Norway, for example, to justify a more liberal wolf killing policy if the wolf population were to have a more favourable conservation status. The larger the wolf population, the more management flexibility the Convention allows. Although the Convention does not directly state how many wolves a country needs to have at a minimum, it is unlikely that maintaining a population in a permanent state of "critically endangered" (its current status on national red lists) satisfies its obligations (Trouwborst et al. 2017b).

The need to document reasoning and utility

There is also an evident need to robustly and openly document the reasoning and utility behind granting exceptions (Box 1). The current Norwegian policy documents (Klima og Miljødepartement 2016) focus very heavily on killing wolves as a means of protecting livestock. However, at least for domestic sheep, this is the one conflict for which there are a whole suite of alternative measures that can be used to prevent conflict. Furthermore, at present the extent of conflicts with livestock within the existing wolf zone is also minimal (Strand 2016; Krange et al. 2016) such that this argumentation is only really relevant for areas outside the zone. In other words, if Norway is to justify a more liberal use of exceptions to kill wolves within the wolf zone it should make the arguments associated with considering other conflicts much more explicitly. This requires an open debate about to what extent it is viewed as principally acceptable to kill wolves to manage perceptions of conflict rather than the material and economic dimensions (e.g. Ericsson et al. 2004) of conflict, and the documentation of the potential utility of this approach. This, in turn, would require a formal acceptance of the legitimacy of invoking the reduction of perceptional and social conflicts as grounds for exceptions (Linnell 2013). This question has both legal (with respect to national and international instruments) and social (public opinion within Norway) dimensions. It is of interest that the Swedish Supreme Administrative Court ruled in favour of recognizing these issues with respect to interpretation of derogations under the Habitats Directive (judgement on 30th December 2016, cases 2406–2408-16 / 2628–2630-16).

Which public?

These other conflicts are much less associated with economic losses and more linked to perceptions, being based on the idea of "tolerance hunting" (Epstein 2017). While the motivation for this has been well documented among many rural stakeholders it is likely to be highly controversial with other sectors of society. It is well known that public tolerance for hunting is linked to the motivations for hunting (Kaltenborn and Brainerd 2016). For example, hunting for meat is often more tolerated than hunting for trophies. Hunting for tolerance is likely to be especially controversial. This implies that it becomes a question of which public interests should be prioritized? Those of certain rural stakeholders or those of a wider society (both rural and urban)? This has been a central part of ongoing controversies in North American wolf management (Treves et al. 2017; Vucetich et al. 2017) and has also become apparent in Norway in recent months. It is, however, important to not confound the desire to kill wolves with an automatic anti-wolf stance (Kaltenborn et al. 2013a.b). Here we note, but do not ourselves address, the ongoing and as yet undecided debate over the compatibility of tolerance hunting with the derogation clause in Article 16 of the Habitats Directive. Whereas the Swedish Supreme Administrative Court, in the aforementioned ruling, accepted hunting as a legally viable option to increase social tolerance of wolves, Epstein (2017) has pointed out that in the absence of clear evidence that allowing hunting indeed delivers wolf conservation results, the CJEU is likely to "interpret the Habitats Directive to prohibit tolerance hunting." Given the Court's prior case law Epstein's prediction may well be correct, but for present purposes we recall that the interpretation of the Bern Convention is not directly affected by this EU case law.

While there are many good arguments for being responsive to the concerns of rural stakeholders who are being asked to share their properties, neighbourhoods, and landscapes with wolves (Redpath et al. 2017) it is essential that management explicitly addresses the question of how they are balancing the concerns of the different publics within the intentions, constraints and obligations imposed by the Convention. The current Norwegian policy, which aims to have high rates of wolf killing and minimal population goals, can hardly be viewed as a reasonable attempt at balancing these interests, and certainly not as living up to the country's obligations under the Bern Convention. As the conflict is presently playing out it is becoming increasingly clear that the main limitation to the flexibility of Norway's wolf management is not with the Convention's strict protection designation, but with the polarized domestic public opinion concerning the moral acceptability of different motivations for killing wolves, and especially with parliament's attempts to set minimal population goals that do not conform to the requirements of Article 2 of the Convention (Trouwborst et al. 2017b).

Strict on goals, flexible on means

Overall, for Bern Convention parties in general and for Norway in particular, the aggregate outcome of our current analysis and our prior analysis of Article 2 (Trouwborst et al. 2017b) underscores that being ambitious and strict on population targets and flexible and pragmatic on the way to achieve them may well be the best way forward for large carnivore conservation and management in the human-dominated landscapes of Europe.

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References

Andersen R, Linnell JDC, Hustad H, Brainerd S (2004) Large carnivores and human communities: a guide to coexistence in the 21st century. Norwegian Institute for Nature Research Temahefte 25: 1–48.

Andersen R, Linnell JDC, Solberg EJ (2006) The future role of large carnivores on terrestrial trophic interactions: the northern temperate view. In: Danell K, Bergström R, Duncan P, Pastor J (Eds) Large herbivore ecology, ecosystem dynamics and conservation. Cambridge University Press, Cambridge, 413–448. https://doi.org/10.1017/CBO9780511617461.016

Bautista C, Naves J, Revilla E, Fernández N, Albrecht J, Scharf AK, Rigg R, Karamanlidis AA, Jerina K, Huber D, Palazón S, Kont R, Ciucci P, Groff C, Dutsov A, Seijas J, Quenette PY, Olszańska A, Shkvyria M, Adamec M, Ozolins J, Jonozovič M, Selva N (2017) Patterns and correlates of claims for brown bear damage on a continental scale. Journal of Applied Ecology 54: 282–292. https://doi.org/10.1111/1365-2664.12708

Bensch S, Andrén H, Hansson B, Pedersen HC, Sand H, Sejberg D, Wabakken P, Åkersson M, Liberg O (2006) Selection for heterozygosity gives hope to a wild population of inbred wolves. Plos One 1: e72. https://doi.org/10.1371/journal.pone.0000072

Bisi J, Kurki S, Svensberg M, Liukkonen T (2007) Human dimensions of wolf (Canis lupus) conflicts in Finland. European Journal of Wildlife Research 53: 304–314. https://doi.org/10.1007/s10344-007-0092-4

Boitani L, Linnell JDC (2015) Bring large mammals back: large carnivores in Europe. In: Pereira HM, Navarro LM (Eds) Rewilding European Landscapes. Springer, Berlin, 67–84.

Borg BL, Arthur SM, Bromen NA, Cassidy KA, McIntyre R, Smith DW, Prugh LR (2016) Implications of Harvest on the Boundaries of Protected Areas for Large Carnivore Viewing Opportunities. Plos One 11. https://doi.org/10.1371/journal.pone.0153808

Bowman M, Davies P, Redgwell C (2010) Lyster's International Wildlife Law, 2nd ed. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511975301

Breitenmoser U, Angst C, Landry JM, Breitenmoser-Würsten C, Linnell JDC, Weber JM (2005) Non-lethal techniques for reducing depredation. In: Woodroffe R, Thirgood S, Rabinowitz A (Eds) People and wildlife: conflict or coexistence? Cambridge University Press, Cambridge, 49–71. https://doi.org/10.1017/CBO9780511614774.005

Butler JRA, Linnell JDC, Morrant D, Athreya V, Lescureux N, McKeown A (2014) Dog eat dog, cat eat dog: social-ecological dimensions and implications of dog predation by wild carnivores. In: Gompper M (Ed.) Free-ranging dogs and wildlife conservation. Oxford University Press, Oxford, 117–143.

Carter NH, Linnell JDC (2016) Co-adaptation is key to coexisting with large carnivores. Trends in Ecology and Evolution 31: 575–578. https://doi.org/10.1016/j.tree.2016.05.006

Chan KMA, Balvanera P, Benessaiah K, Chapman M, Diaz S, Gomez-Baggethun E, Gould R, Hannahs N, Jax K, Klain S, Luck GW, Martin-Lopez B, Muraca B, Norton B, Ott K, Pascual U, Satterfield T, Tadaki M, Taggart J, Turner N (2016) Why protect nature? Rethinking values and the environment. Proceedings of the National Academy of Sciences of the United States of America 113: 1462–1465. https://doi.org/10.1073/pnas.1525002113

Chapron G, Kaczensky P, Linnell JDC, von Arx M, Huber D, Andrén H, López-Bao JV, Adamec M, Álvares F, Anders O, Balčiauskas L, Balys V, Bedő P, Bego F, Blanco JC, Breitenmoser U, Brøseth H, Bufka L, Bunikyte R, Ciucci P, Dutsov A, Engleder T, Fuxjäger C, Groff C, Holmala K, Hoxha B, Iliopoulos Y, Ionescu O, Jeremić J, Jerina K, Kluth G, Knauer F, Kojola I, Kos I, Krofel M, Kubala J, Kunovac S, Kusak J, Kutal M, Liberg O, Majić A, Männil P, Manz R, Marboutin E, Marucco F, Melovski D, Mersini K, Mertzanis Y, Mysłajek RW, Nowak S, Odden J, Ozolins J, Palomero G, Paunović M, Persson J, Potočnik H, Quenette P-Y, Rauer G, Reinhardt I, Rigg R, Ryser A, Salvatori V, Skrbinšek T, Stojanov A, Swenson JE, Szemethy L, Trajçe A, Tsingarska-Sedefcheva E, Váňa M, Veeroja R, Wabakken P, Wölfl M, Wölfl S, Zimmermann F, Zlatanova D, Boitani L (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346: 1517–1519. https://doi.org/10.1126/science.1257553

Chapron G, Treves A (2016) Blood does not buy goodwill: allowing culling increases poaching of a large carnivore. Proceedings of the Royal Society B-Biological Sciences 283. https://doi.org/10.1098/rspb.2015.2939

Cromsigt J, Kuijper DPJ, Adam M, Beschta RL, Churski M, Eycott A, Kerley GIH, Mysterud A, Schmidt K, West K (2013) Hunting for fear: innovating management of human-wildlife conflicts. Journal of Applied Ecology 50: 544–549. https://doi.org/10.1111/1365-2664.12076

Darpö J, Epstein Y (2015) Under fire from all directions: Swedish wolf management hunting scrutinized by Brussels and at home. In: Born C et al. (Eds) The Habitats Directive in its EU environmental law context. Routledge, London, 348–372.

Eklund A et al. (2017) Limited evidence on the effectiveness of interventions to reduce livestock predation by large carnivores. Scientific Reports 7: 2097. https://doi.org/10.1038/s41598-017-02323-w

Epstein Y (2014) The Habitats Directive and Bern Convention: synergy and dysfunction in public international and EU law. Georgetown International Environmental Law Review 26: 139–173.

Epstein Y (2017) Killing wolves to save them? Legal responses to "tolerance" hunting in the European Union and United States. Review of European Community and International Environmental Law 26: in press. https://doi.org/10.1111/reel.12188

Ericsson G, Heberlein TA (2003) Attitudes of hunters, locals, and the general public in Sweden now that the wolves are back. Biological Conservation 111: 149–159. https://doi.org/10.1016/S0006-3207(02)00258-6

Ericsson G, Heberlein TA, Karlsson J, Bjärvall A, Lundvall A (2004) Support for hunting as a means of wolf Canis lupus population control in Sweden. Wildlife Biology 10: 260–276.

Fischer A, Sandström C, Delibes-Mateos M, Arroyo B, Tadie D, Randall D, Hailu F, Lowassa A, Msuha M, Kereži V, Reljić S, Linnell J, Majić A (2013) On the multifunctionality of hunting – an institutional analysis of eight cases from Europe and Africa. Journal of Environmental Planning and Management 56: 531–552. https://doi.org/10.1080/09640568.2012.689615

Fleurke FM, Trouwborst A (2014) European regional approaches to the transboundary conservation of biodiversity: the Bern Convention and the EU Birds and Habitats Directives. In: Kotze L, Marauhn T (Eds) Transboundary governance of biodiversity. Martinus Nijhoff Publishers, Leiden/Boston, 128–162.

Herfindal I, Linnell JDC, Moa PF, Odden J, Austmo LB, Andersen R (2005) Does recreational hunting of lynx reduce depredation losses of domestic sheep. Journal of Wildlife Management 69: 1034–1042. https://doi.org/10.2193/0022-541X(2005)069[1034:DRHOLR]2.0.CO;2

Hiedanpaa J (2013) Institutional Misfits: Law and Habits in Finnish Wolf Policy. Ecology and Society 18. https://doi.org/10.5751/es-05302-180124

Hiedanpaa J, Bromley DW (2013) The Stakeholder Game: Pleadings and Reasons in Environmental Policy. Journal of Speculative Philosophy 27: 425–441. https://doi.org/10.5325/jspecphil.27.4.0425

Hiedanpää J, Bromley DW (2011) The harmonization game: reasons and rules in European biodiversity policy. Environmental Policy and Governance 21: 99–111. https://doi.org/10.1002/eet.561

Huber J, Von Arx M, Bürki R, Manz R, Breitenmoser U (2016) Wolves living in proximity to humans. KORA Bericht Nr 76: 1–19. https://doi.org/10.1016/j.biocon.2016.08.041

Jacobsen KS, Linnell JDC (2016) Perceptions of environmental justice and the conflict surrounding large carnivore management in Norway - Implications for conflict management. Biological Conservation 203: 197–206. https://doi.org/10.1016/j.biocon.2016.08.041

Kaltenborn B, Brainerd SM (2016) Can poaching inadvertently contribute to increased public acceptance of wolves in Scandinavia. European Journal of Wildlife Research 62: 179–188. https://doi.org/10.1007/s10344-016-0991-3

Kaltenborn BP, Andersen O, Linnell JDC (2013a) Predators, stewards, or sportsmen – how do Norwegian hunters perceive their role in carnivore management? International Journal of Biodiversity Science, Ecosystem Services and Management 9: 239–248.

Kaltenborn BP, Andersen O, Linnell JDC (2013b) Is hunting large carnivores different from hunting ungulates? Some judgments made by Norwegian hunters. Journal for Nature Conservation 21: 326–333. https://doi.org/10.1016/j.jnc.2013.05.004

Klima og Miljødepartement (2016) Ulv i norsk natur: bestandsmål for ulv og ulvesone. Klima og Miljødepartement, Oslo, Norway, 132 pp.

Knott EJ, Bunnefeld N, Huber D, Reljic S, Kereži V, Milner-Gulland EJ (2014) The potential impacts of changes in bear hunting policy for hunting organisations in Croatia. European Journal of Wildlife Research 60: 85–97. https://doi.org/10.1007/s10344-013-0754-3

Kojola I, Ronkainen S, Hakala A, Heikkinen S, Kokko S (2004) Interactions between wolves Canis lupus and dogs C. familiaris in Finland. Wildlife Biology 10: 101–106.

Krange O, Odden J, Skogen K, Linnell JDC, Stokland HB, Vang S, Mattisson J (2016) Evaluering av regional rovviltforvaltning. NINA Rapport 1268, 194 pp.

Linnell JDC (2013) From conflict to coexistence: insights from multi-disciplinary research into the relationships between people, large carnivores and institutions. Istituto di Ecologia Applicata, Rome.

Linnell JDC, Alleau J (2015) Predators that kill humans: myth, reality, context and the politics of wolf attacks on people. In: Angelici FM (Ed.) Problematic wildlife - a cross-dispclinary approach. Springer, Berlin, 357–372.

Linnell JDC, Aanes R, Swenson JE, Odden J, Smith ME (1997) Translocation of carnivores as a method for managing problem animals: a review. Biodiversity and Conservation 6: 1245–1257. https://doi.org/10.1023/B:BIOC.0000034011.05412.cd

Linnell JDC, Boitani L (2012) Building biological realism into wolf management policy: the development of the population approach in Europe. Hystrix - Italian Journal of Mammalogy 23: 80–91.

Linnell JDC, Breitenmoser U, Breitenmoser-Würsten C, Odden J, von Arx M (2009) Recovery of Eurasian lynx in Europe: what part has reintroduction played? In: Hayward MW, Somers MJ (Eds) Reintroduction of top-order predators. Wiley-Blackwell, Oxford, 72–91. https://doi.org/10.1002/9781444312034.ch4

Linnell JDC, Brøseth H, Odden J, Nilsen EB (2010) Sustainably harvesting a large carnivore? Development of Eurasian lynx populations in Norway during 160 years of shifting policy. Environmental Management 45: 1142–1154. https://doi.org/10.1007/s00267-010-9455-9

Linnell JDC, Kaczensky P, Wotschikowsky U, Lescureux N, Boitani L (2015) Framing the relationship between people and nature in the context of European nature conservation. Conservation Biology 29: 978–985. https://doi.org/10.1111/cobi.12534

Linnell JDC, Odden J, Mertens A (2012) Mitigation methods for conflicts associated with carnivore depredation on livestock. In: Boitani L, Powell RA (Eds) Carnivore ecology and conservation: a handbook of techniques. Oxford University Press, Oxford, 314–332. https://doi.org/10.1093/acprof:oso/9780199558520.003.0014

Linnell JDC, Odden J, Smith ME, Aanes R, Swenson JE (1999) Large carnivores that kill livestock: do "problem individuals" really exist? Wildlife Society Bulletin 27: 698–705.

Linnell JDC, Salvatori V, Boitani L (2008) Guidelines for population level management plans for large carnivores in Europe. A Large Carnivore Initiative for Europe report prepared for the European Commission (contract 070501/2005/424162/MAR/B2), 85 pp.

Linnell JDC, Zachos FE (2011) Status and distribution patterns of European ungulates: genetics, population history and conservation. In: Putman R, Apollonio M, Andersen R (Eds) Ungulate management in Europe: problems and practices. Cambridge University Press, Cambridge, 12–53. https://doi.org/10.1017/CBO9780511974137.003

Mabille G, Stien A, Tveraa T, Mysterud A, Broseth H, Linnell JDC (2015) Sheep farming and large carnivores: What are the factors influencing claimed losses? Ecosphere 6: Article 82. https://doi.org/10.1890/es14-00444.1

Mace GM (2014) Whose conservation? Science 345: 1558–1560. https://doi.org/10.1126/science.1254704

Madden F, McQuinn B (2014) Conservation's blind spot: the case for conflict transformation in wildlife conservation. Biological Conservation 178: 97–106. https://doi.org/10.1016/j.biocon.2014.07.015

Majic A, de Bodonia AMT, Huber D, Bunnefeld N (2011) Dynamics of public attitudes toward bears and the role of bear hunting in Croatia. Biological Conservation 144: 3018–3027. https://doi.org/10.1016/j.biocon.2011.09.005

Maser C, Polio CA (2012) Resolving environmental conflicts. CRC Press, London, 241 pp.

Miljøverndepartementet (1992) White paper on the management on bears, wolverine, wolf and lynx in Norway [Om forvaltning av bjørn, jerv, ulv og gaupe (Rovviltmeldingen)]. Stortingsmeldingen 27–1991–92: 54.

Miljøverndepartementet (1997) On large carnivore management [Om rovviltforvalting]. Stortingsmelding 35–1996–1997.

Miljøverndepartementet (2003) Carnivores in Norwegian nature [Rovvilt i norsk natur]. Stortingsmelding 15–2003–2004, 134.

Olson ER, Stenglein JL, Shelley V, Rissman AR, Browne-Nunez C, Voyles Z, Wydeven AP, Van Deelen T (2015) Pendulum swings in wolf management led to conflict, illegal Kills, and a legislated wolf hunt. Conservation Letters 8: 351–360. https://doi.org/10.1111/conl.12141

Penteriani V et al. (2016) "Human behaviour can trigger large carnivore attacks in developed countries." Scientific Reports 6. https://doi.org/10.1038/srep20552

Redpath S, Linnell JDC, Festa-Bianchet M, Boitani L, Bunnefeld N, Gutiérrez RJ, Irvine J, Johansson M, McMahon BJ, Pooley S, Sandstrom C, Sjölander-Lindqvist A, Skogen K, Swenson JE, Trouwborst A, Young J, Milner-Gulland EJ (2017) Don't forget to look down - collaborative approaches to predator conservation. Biological Reviews in press. https://doi.org/10.1111/brv.12326

Redpath SM, Young J, Evely A, Adams WM, Sutherland WJ, Whitehouse A, Amar A, Lambert RA, Linnell JDC, Watt A, Gutierrez RJ (2013) Understanding and managing conservation conflicts. Trends Ecol Evol 28: 100–109. https://doi.org/10.1016/j.tree.2012.08.021

Reed MS (2008) Stakeholder participation for environmental management: a literature review. Biological Conservation 141: 2417–2431. https://doi.org/10.1016/j.biocon.2008.07.014

Rosen T, Bath A (2009) Transboundary management of large carnivores in Europe: from incident to opportunity. Conservation Letters 2: 109–114. https://doi.org/10.1111/j.1755-263X.2009.00054.x

Røskaft E, Bjerke T, Kaltenborn BP, Linnell JDC (2003) Patterns of self-reported fear towards large carnivores among the Norwegian public. Evolution and Human Behaviour 24: 184–198. https://doi.org/10.1016/S1090-5138(03)00011-4

Salvatori V, Linnell JDC (2005) Report on the conservation status and threats for wolf (Canis lupus) in Europe. Council of Europe Report T-PVS/Inf (2005) 16, 24 pp.

Sandström C, Pellikka J, Ratamäki O, Sande A (2009) Management of large carnivores in Fennoscandia: new patterns of regional participation. Human Dimensions of Wildlife 14: 37–50. https://doi.org/10.1080/10871200802304726

Skogen K, Krange O (2003) "A wolf at the gate: The anti-carnivore alliance and the symbolic construction of community." Sociologia Ruralis 43(3): 309–325. https://doi.org/10.1111/1467-9523.00247

Skogen K, Krange O, Figari H (2013) Ulvekonflikter: en sosiologisk studie. Akademika forlag, Oslo, 270 pp.

Skogen K, Mauz I, Krange O (2006) "Wolves and Eco-power. A French-Norwegian Analysis of the Narratives of the Return of Large Carnivores." Journal of Alpine Research 94(4): 78–87. https://doi.org/10.3406/rga.2006.5593

Starling MJ, Branson N, Thomson PC, McGreevy PD (2013) "Boldness" in the domestic dog differs among breeds and breed groups. Behavioural Processes 97: 53–62. https://doi.org/10.1016/j.beproc.2013.04.008

Strand GH (2016) Rovviltbestandenes betydning for landbruk og matproduksjon basert på norske ressurser. NIBIO 2/63/2016, 128 pp.

Swenson JE, Sandegren F, Bjärvall A, Wabakken P (1998) Living with success: research needs for an expanding brown bear population. Ursus, International Conference on Bear Research and Management 10: 17–23.

Treves A, Krofel M, McManus J (2016) Predator control should not be a shot in the dark. Frontiers in Ecology and the Environment 14: 380–388. https://doi.org/10.1002/fee.1312

Trouwborst A (2010) Managing the carnivore comeback: international and EU species protection law and the return of lynx, wolf and bear to western Europe. Journal of Environmental Law 22: 347–372. https://doi.org/10.1093/jel/eqq013

Trouwborst A (2015a) Global large carnivore conservation and international law. Biodiversity and Conservation 24: 1567–1588. https://doi.org/10.1007/s10531-015-0894-8

Trouwborst A (2015b) Law and conservation conflicts. In: Redpath SM, Gutiérrez RJ, Wood KA, Young JC (Eds) Conflicts in conservation: navigating towards solutions. Cambridge University Press, Cambridge, 108–118. https://doi.org/10.1017/CBO9781139084574.009

Trouwborst A, Boitani L, Linnell JDC (2017a) Interpreting 'favourable conservation status' for large carnivores in Europe: how many are needed and how many are wanted? Biodiversity and Conservation 26: 37–61. https://doi.org/10.1007/s10531-016-1238-z

Trouwborst A, Fleurke F, Linnell JDC (2017b) Norway's Wolf Policy and the Bern Convention on European Wildlife: Avoiding the "Manifestly Absurd". Journal of International Wildlife Law & Policy in press.

Tveraa T, Stien A, Broseth H, Yoccoz NG (2014) The role of predation and food limitation on claims for compensation, reindeer demography and population dynamics. Journal of Applied Ecology 51: 1264–1272. https://doi.org/10.1111/1365-2664.12322

Vucetich JA, Bruskotter JT, Nelson MP, Peterson RO, Bump JK (2017) Evaluating the principles of wildlife conservation: a case study of wolf (Canis lupus) hunting in Michigan, United States. Journal of Mammalogy 98: 53–64.

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RESPONSE

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A critical comment to D´Cruze and Macdonald (2016)

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It was with great expectations that we started reading D´Cruze and Macdonald (2016), since the analysis of illicit global wildlife trade (IWT) has strong implications on the evaluation of global trends and the level of commitment of national authorities to this important issue. Therefore, we completely agree with the scope of this article and the option to focus on the IWT of live specimens, due to its pertinence. However, we believe that unintentional biased analysis decisions may have led to erroneous conclusions. Since the subject of the article has a broad conservation audience we think it is important to critically discuss the implications.

Our main comment concerns the queries applied to the original data set, and their implications on the results. The authors used the information publicly available in the CITES Trade Database (CITES 2013). This database lists all records of legal imports and exports of products or specimens of species listed under the CITES convention. It is curated by UNEP-WCMC on behalf of the CITES Secretariat and is based on the reports that are submitted annually by the CITES convention countries (currently 183 countries).

In D´Cruze and Macdonald (2016) the CITES Trade Database was queried for “all live wild animal seizures for the years 2010-2014 inclusive” and “specifically requested data only using the LIVE trade term and the CITES source code I”. The authors used this query to select “illegal trade seizure records of live animals as outlined in Notification 2002/022 (UNEP-WCMC 2014)”.

In the CITES Trade Database the "source" field presents several codes used to indicate the "original source" (e.g., captive-bred, farmed, wild specimens or those that have been confiscated or seized) of the traded specimens. As the most recent guidelines (distributed with Notification 2017/006) clearly state: "… as well as specimens that were seized or confiscated in a previous shipment, that are now being legally traded for legitimate purposes such as the return of confiscated specimens or a forensic analysis to be done in the importing country, etc. In these cases, source code "I" should be used and these records should be included within the annual report". Therefore, the records used by D´Cruze and Macdonald (2016) are only a small and possibly biased subset of all specimens seized and/or confiscated. When they are not euthanized and survive the confiscation and holding process, many seized specimens are not repatriated and may be resold in the domestic market. On the other hand, many times only valuable specimens will be repatriated or sold to another country and registered on the CITES annual reports. Additionally, the information concerning the history of seizures can be amiss concerning the roles of the importer and exporter countries. If you erroneously interpret these records as seizures and not as trade of seized items, their roles will be reversed. In reality, the exporter will be the country where the seizure took place (only when seizures occur before leaving the country this refers to the country of origin) and the importer will be the country of destination (only when seized specimens are repatriated, this will be the country of origin).

It is easy to understand how this misunderstanding can be made, since the way this information is outlined in older guidelines (latest distributed with Notification 2011/019) can lead to misinterpretations on this subject. In these guidelines for the preparation and submission of CITES annual reports "This column should also be used to indicate specimens seized, confiscated or illegally traded". Records with source "I" may be interpreted not as a trade record but as a seizure record. Therefore, the CITES Trade Database, the only public database on wildlife trade, does not reflect the overall number of seizures concerning traffic of live specimens of CITES listed species.

Some IWT can be detected on this database (Broad et al. 2003) by comparing data from importing and exporting countries or in the case mentioned above (legal trade of specimens that were seized or confiscated in a previous shipment). In the case of the author's own dataset, unfortunately the number of records with both types of information is less than 4% and only in one record the number of specimens does not match between the importer and exporter reports. The authors also state that "currently it is not possible to establish how many seized wild animals have re-entered commercial trade". This is true in the case of domestic resale within the country of seizure, but international resale could be estimated using data from the CITES Trade Database.

We consider this comment very important to aid other researchers willing to use the same kind of data and queries. It is also important for readers not familiar with the CITES Trade Database and its regulations to understand the implications and biases of this approach. To our knowledge, the only similar analysis produced in recent years (UNODC 2016) was performed under the auspices of the UNODC (United Nations Office on Drugs and Crime) that is responsible for the World Wildlife Seizure database (World Wise). This analysis used data from different sources, most of them not available for public consultation. The reasons for the non-availability of information are multiple, ranging from confidentiality due to pending legal processes to prevention of erroneous conclusions, since seizure statistics can be positively correlated to better law enforcement or to real IWT numbers (Reeve 2002).

In the World Wildlife Seizure database, the information obtained from CITES annual, biennial and special reports constitutes 34% of all data from the 2005-2014 period. Most of this data is compiled from the Biennial Reports, which contain information on efforts to implement the convention, including law enforcement data on seizures. According to UNODC (2016), only some countries include seizure data in their annual reports, as separate tables from the tables of legal trade, that are not included into the CITES Trade Database.

In conclusion, we advise that any analysis based on the CITES Trade Database should take into account that it refers to legal trade and the amount of data concerning illegal trade is limited by the very nature of the database and the main source of data, the annual CITEs reports. To overcome these issues and considering the importance of seizure data to analyze the dynamics of IWT, CITES is performing a major revision on the data that is necessary to be delivered on the annual reports. At its 66th meeting (Geneva, January 2016), the CITES Standing Committee adopted a new annual illegal trade report (Notification 2016/007). The first annual illegal trade report is due on 31 October 2017, covering data from 2016 and will provide information on the specimen and also on country of origin and countries of transit. This is a major achievement that will have surely a major impact on the prevention of IWT in the near future.

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References

CITES (2013) A guide to using the CITES Trade Database, version 8. United Nations Environment Programme & World Conservation Monitoring Centre.

D´Cruze N, Macdonald DW (2016) A review of global trends in CITES live wildlife confiscations. Nature Conservation 15: 47–63. https://doi.org/10.3897/natureconservation.15.10005

Broad S, Mulliken T, Roe D (2003) The Nature and Extent of Legal and Illegal Trade in Wildlife rates. In: Oldfield S (Eds) The Trade in Wildlife: Regulation for Conservation. Earthscan Publications Ltd, London, 3–22.

Reeve R (2002) Policing International Trade in Endangered Species: The CITES Treaty and Compliance. The Royal Institute of International Affairs & Earthscan, London.

UNODC (2016) World Wildlife Crime Report: Trafficking in protected species. United Nations Publication, New York.

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RESPONSE

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An update on CITES live confiscations, in response to Lopes et al. (2017)

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We are pleased that Lopes et al. (2017), approached our article with high expectations and thank them for their fulsome endorsement of the importance of the topic. We are also grateful that their criticism of our use of CITES source code 'I' provides us with an opportunity to clarify how things have changed since we wrote our article (D'Cruze and Macdonald 2016). Indeed, insofar as a superficial reader might have construed Lopes et al.'s (2017) commentary as a criticism of our paper, our response might be unexpected in that we agree with much of what they write. However, we differ from them in the conclusion that subsequent developments have weakened the essence of our main conclusion; on the contrary, we think they strengthen it. Our main conclusion was, and remains, that CITES trade database records are inconsistent and incomplete, with data on the disposal of confiscated live animals lacking, and that these deficiencies impede the proper allocation of available resources and prevent the effective monitoring and evaluation of management outcomes. More generally, by drawing attention to uncertainties in the fate of large numbers of confiscated wild animals, threatened or otherwise, we believe our paper has fulfilled an important role.

Lopes et al. (2017), correctly, and helpfully, draw attention to the fact that the CITES source code 'I' should represent legal (re)exports of seized wild animals and their derivatives using a CITES permit, rather than seizures relating to illegal trade activity, as we had used it. They correctly state that we followed an earlier version of the official CITES guidelines [Version 8 (UNEP-WCMC 2014)] to interpret the CITES Trade Database. This was, of course, our only option insofar as it was only several months after our paper was published that the latest clarifying guidelines for the preparation and submission of CITES annual reports became publically available (via CITES Notification 2017/006), followed one month later by a new guide to the application of CITES source codes (UNEP-WCMC 2017). Together, these documents added new clarity, revealing ambiguity in the guidelines at the time we wrote and published our paper. In passing, we observe sadly that instances of such misleading failures of clarity detract seriously from the usefulness of the CITES database, and the one exposed here is not the only such case [one of us has recently noted unhelpful ambiguity in the figures relating to legal lion trophy exports, and recommended a reform of this (Macdonald 2016)].

Like Lopes et al. (2017), we think it helpful to excavate further the intricacies of the CITES database and its interpretation. As they correctly state, the CITES trade database should only contain legal trade data, reported via granted permits and certificates (as specified in Article VIII of the Convention, paragraph 6 and 7). However, it has become clear that this is not always the case. For example, Parties are sometimes also required to report seizures involving illegal wildlife trade [e.g. Pangolins (*Pholiodota*) as requested through Decisions 16.41 and 16.42 in 2013 (CITES 2013)]. Indeed, according to Heinrich et al., (2016) [also published subsequent to D'Cruze and Macdonald (2016)] the USA is one of the few countries reporting such trafficking incidents, and we understand that it does this by reporting the seizures under source code 'I' in the source column [their study reports 98% of pangolin records using source code 'I' made between 1975 and 2014 proved to be seizures rather than re(exports)].

Acknowledging that source code 'I' has been, and is mostly likely still being, misinterpreted and used by different Parties in different ways, further shakes confidence in the CITES Trade Database that has already been subject to criticism due to claims of inconsistent and incomplete reporting by Parties (e.g. Harrington et al. 2014; UNEP-WCMC 2014; Heinrich et al. 2016). These misgivings, and the explicit acknowledgement that data assigned to Code 'I' have been and remain a mixture (of unknown proportions) of both illegal seizure and legal re(export) incidents, seem to strengthen the conclusions and recommendations we offered in D'Cruze and Macdonald (2016) and we repeat our gratitude to Lopes et al. (2017), for affording us the opportunity to point this out.

In light of the clarity provided via CITES Notification 2017/006, and given the increased ambiguity regarding what type of incidents have been assigned to CITES source code 'I', we conclude that currently it remains impossible, using the CITES Trade Database alone, to establish accurately how many seized wild animals have re-entered commercial trade. Rather, as exemplified by Heinrich et al., (2016) in the case of pangolins, we argue that to establish this number it is necessary to compare these records with information in other databases that contain data regarding illegal wildlife seizures [e.g. the Law Enforcement Management Information System (LEMIS) database maintained in USA]. Similarly, as highlighted by Lopes et al. (2017), it is now clear that the true role of the importer and exporter is also impossible to determine without similar comparisons to other existing databases. Transparency is further obscured insofar as these additional data may be hard to access.

Standing by our original conclusion, and further strengthened by ambiguity in interpreting the CITES data, the point remains that national enforcement agencies have had to detect and quickly deal with illegal live shipments involving a diverse array of vertebrate species, and (as reaffirmed by Lopes et al. 2017) that numbers reported are likely the 'tip of a far bigger iceberg'. It also remains true that CITES Trade Database records are inconsistent and incomplete. Indeed, data regarding the disposal of confiscated live animals is unavailable as providing them is not currently a formal CITES requirement. We repeat our conclusion that this lack of information impedes the proper allocation of resources and prevents the effective monitoring and evaluation of management outcomes. We add now, although we had imagined that it was obvious, that this is detrimental for both conservation and animal welfare.

We welcome the news that the first CITES annual illegal trade report will be made public in October 2017. Lopes et al. (2017) are surely right that this document will provide valuable information that will aid efforts to combat illegal wildlife trade. However, this diminishes neither the veracity of our main conclusions, nor the relevance of recommendations provided in D'Cruze and Macdonald (2016) which we presented formally at the 17th Conference of the Parties during a side event opened by the CITES Secretary General in September 2016. We are pleased to consider that our work may have helped to prompt, soon after, the adoption of Resolution Conf. 17.8 on Disposal of illegally traded and confiscated specimens of CITES-listed species (CITES Notification 2017/045). This led in turn, again pleasingly, to the development of a questionnaire intended to review existing guidelines and evaluate current practice in the disposal of confiscated live wild animals.

Both of these policy-focused developments represent significant leaps forward, but alone they will be insufficient to ensure the accuracy of reporting required to monitor illegal wildlife trade or to guide the allocation of available resources to address it. The publication of D'Cruze and Macdonald (2016) and subsequent documents thereafter (CITES Notification 2017/006; Heinrich et al. 2016; UNEP-WCMC 2017) have also contributed, we think usefully, to the accumulating evidence of opportunities to improve the already unquestionably valuable CITES data and to reduce confusion amongst Parties and researchers regarding reporting requirements.

However, given past evidence of inconsistent and incomplete reporting by Parties, and indeed the comments made by Lopes et al. (2017), future records using source code 'I' should be subject to scrutiny before judgement can be reached on whether such initiatives have been successful in preventing further misinterpretation. Meanwhile, none of the foregoing detracts from our general assertion that a very large number of Threatened wild animals is confiscated each year, that they must inevitably place a heavy burden on confiscating authorities, that they constitute a detriment to both conservation and welfare, with many of their fates remaining unknown and unrecorded. While it is appropriate that specialists (like Lopes et al. 2017, and ourselves) delve into the minutiae of these figures, our shared quest for precision should not obscure the starkness of this situation.

References

CITES (2013) Decisions 16.41 and 16.42. Sixteenth Meeting of the Conference of Parties. Bangkok, Thailand.

D'Cruze N, Macdonald DW (2016) A review of global trends in CITES live wildlife confiscations. Nature Conservation 15: 47–63. https://doi.org/10.3897/natureconservation.15.10005

Harrington LA (2015) International commercial trade in live carnivores and primates 2006–2012: response to Bush et al. 2014. Conservation Biology 29: 293–296. https://doi.org/10.1111/cobi.12448

Heinrich S, Wittmann TA, Prowse TAA, Ross JV, Delean S, Shepherd CR, Cassey P (2016) Where did all the pangolins go? Global Ecology and Conservation 8 241–253. https://doi.org/10.1016/j.gecco.2016.09.007

Lopes RJ, Ferreira JM, Moraes-Barros N (2017) A critical comment to D´Cruze and Macdonald (2016). Nature Conservation 21: 159–161. https://doi.org/10.3897/natureconservation.21.13071

Macdonald DW (2016) Report on lion conservation with particular reference to the issue of trophy hunting. Wildlife Conservation Research Unit 2016: 1–63. https://www.wildcru.org/wp-content/uploads/2016/12/Report_on_lion_conservation.pdf

UNEP-WCMC (2014) A guide to using the CITES Trade Database, version 8. United Nations Environment Program, World Conservation Monitoring Centre, 1–21.

UNEP-WCMC (2017) A guide to the application of CITES source codes, version 1. United Nations Environment Program, World Conservation Monitoring Centre, 1–17.