RESEARCH ARTICLE



Nomen omen. Toponyms predict recolonization and extinction patterns for large carnivores

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Abstract

The names given to places are a legacy of the past distribution of animal and plant species. The hypothesis tested in this work is that the density of toponyms can be used to predict the range of two large and charismatic species over time: the wolf and the brown bear in Italy. Kernel density maps of the toponyms were created and different thresholds of density were overlapped with the present and the historical ranges for both species. The density level maps were tested with the Kappa statistics against available historical ranges for both species. The pattern of the density in toponyms overlapped with the pattern of contraction and expansion reported in literature for both species over time. The minimum historical distributions of wolves and brown bears occurred at the highest densities of toponyms (95% isopleth value) and, overall, the various kernels thresholds showed an excellent agreement with the historical maps with an average Kappa of 0.84 ± 0.5 .

Keywords

Brown bear, wolf, Italy, historical distribution, home range

Introduction

A toponym is the name given to a geographic place; it is a word of Greek origin from the combination of the terms *tòpos* "place" and *ònoma* "name". The name given to places usually reflects the usage, the most striking natural features, property or particular historical events.

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Studies about the geographical distribution of toponyms are common in historical, archaeological and linguistic research (Cox et al. 2002) and have been used to reconstruct the displacement of human populations in the past, according to the fragments of the different languages that are still present in the names.

Toponyms with explicit reference to animal and plants were given according to what people used to see in their everyday life, thus names can be considered indicators of the former presence of certain species (Aybes and Yalden 1995; Boisseau and Yalden 1998; Gruezo 1999; Hough 2008). The toponyms referring to nature are labelled as phyto-toponyms, when they refer to plants, and zoo-toponyms in the case of animals. Plant common names used in toponyms depict also the usage of the species as food, medicine, fabric or for other activities (Gruezo 1999; Fagúndez and Izco 2016). Place names related to nature are not only a legacy of the former presence of species, but also provide insights about the traditional usage and interaction with the environment. According to Fagúndez and Izco (2016), toponyms are: "stable, spatially-explicit elements that may be used as indicators of bio-cultural diversity", revealing the socio-economic value given to Nature over time and therefore should be considered an important part of cultural heritage. In Europe, research about place names has been used to track recent climate changes and perceptions of those changes (Sousa and García-Murillo 2001; Sweeney et al. 2007; Sousa et al. 2010).

This study focuses on zoo-toponyms and how their occurrence can be used to infer the past distributions of wildlife. Despite the huge amount of information available in names and the importance of knowing the past distribution of the species and habitats for conservation purposes, only a limited number of studies have engaged in reconstructing bio-geographical ranges of occurrence based on toponyms. The reasons are several: the main one is that only the larger or more charismatic species have places named after them (Cox et al. 2002), meaning that only the historical presence of some mammals and birds can be inferred from toponyms. Aybes and Yalden (1995) mapped historical wolf (Canis lupus) and beaver (Castor fiber) distributions in Britain from place names only, while Poole (2015) used toponyms together with bones and other remains found at archaeological sites to infer the past presence of foxes (Vulpes vuples) and badgers (Meles meles). The latter approach was used by Boisseau and Yalden (1998) to reconstruct the crane (Grus grus) presence in the UK and they also demonstrated that this bird used to nest in England. The above mentioned species, in addition to being medium-large sized, do not have any similar looking animals in their range with which they could be confused. In fact, not all common names can be precisely referred to a single species. Two or more species that have a similar appearance can share the same common name: for example the word "deer" can refer to both the red deer and roe deer, as well as the word "eagle" which can identify various species of raptors (Hough 2008; Evans et al. 2012). Another issue in the use of toponyms in bio-geography is that the collaboration with a professional linguistic scholar may be necessary to extract the root of the names from different and old languages (Moore 2002). Last but not least, a distribution inferred from toponyms only can have some limits in the interpretation, if not validated with habitat availability, (Webster 2001; Evans et al. 2012), field evidence such as bones (Boisseau and Yalden 1998) or artefacts and manuscripts.

All the above cited studies produced point maps of the past presence of the species and did not apply any further spatial processing to the toponyms. On the other hand, Cox et al. (2002) calculated the density of the place names to obtain areas of distribution that were later overlapped with the historical occurrence of 21 mammals, 2 snakes and one bird. Among the literature examined, this study was the only one providing a quantitative estimation of the overlap of historical ranges with place names derived distributions. In the present work I further develop the approach of Cox et al. (2002) by using different thresholds of density probability and compare them with different historical ranges at different times.

In Italy, where this study was carried out, there are many examples of phyto and zoo-toponyms (Nocentini 2004). Some examples taken from the plant kingdom include: "Rovereto, Roverè" from the presence of oak species (*Quercus petraea* and *Q. pubescens*) Rovere and Roverella in Italian) and the city of Avellino named after the hazelnut tree (*Corylus avellana*). To illustrate names from the animal kingdom there is "Cervara", which means a place used for hunting deers (*Cervo* in Italian); "Pescara" and "Pescaia" are instead fishing spots, deriving from *Pesce*-fish in Italian), "L'Aquila" a city named "The Eagle". Charismatic animals, such as predators and large mammals, are more likely to have been chosen for place names and they also occur in many flags and town emblems across Italy (Rome is one such example, its symbol being a female wolf nursing the twins Romolo and Remo that later founded the city).

This study focuses on two charismatic species, the brown bear and the wolf, not mistakable for other wildlife and for which historical distributions from field data are available in the Italian Peninsula. If the places were named according to the real presence of the species, we can expect that the names occur more often where the species was present in higher numbers and/or over a longer period of time.

Under this hypothesis, the frequency of the names can be a proxy for the density, thus we can expect that wolves and bears more likely survived in those hotspots of toponyms when their population decreased due to direct persecution over past centuries (Chapron et al. 2014). Similarly, when the carnivore populations increased again due to socio-economic change and afforestation (Ciolli et al. 2012; Ferretti et al. 2018) we expect that the recoloniszation pattern would follow the toponym density.

The aims of this work are to: 1) create maps of the place names linked to the Wolf (*Canis lupus*) -*Lupo*- in Italian and to the two subspecies of Brown bear -*Orso*- that occur in Italy, the European brown bear and the Marsican brown bear (*Ursus arctos arctos arctos and Ursus arctos marsicanus*), the latter is an Italian endemism; 2) compare the distributions derived from the toponyms with present and past ranges of the two mammals; 3) explore the knowledge and the perception of those carnivores.

Material and methods

A list of the dialectal names for bear and wolf in the various Italian regions were retrieved from the on-line dictionary of the Italian dialects (http://ww.dialettando.com).

Open Street Map (OSM) and the map of the Italian toponyms map (PCN) were queried with the words or pattern of letters from the previously identified list. The queries were then refined by semi-automatic selection of the relevant place names, removing obvious artefacts of the queries, such as names of restaurants or family names. The place names were later categorised in three ways: according to the features they described (such as mountains, rivers, settlements...), if any; according to gender, i.e. masculine and feminine names; and finally according to their positive or negative connotation. Toponyms were labelled as negative terms if they identified hunting places, made clear reference to injury and/or death or were pejorative declinations of the name. Reference to cubs, terms of endearment and diminutives were deemed obvious positive connotations. The simple attribution of a name to a landscape element was considered as neutral, even if it is undoubtedly a sign of emotional connection with the species. The complete list of the data used for this work is available in Table 1, which also reports some additional information about the resolution and the process that was necessary before using it. Some maps were already available in digital format suitable for the GIS environment, while others were digitised from digital images. Some sources reported only the presence of the species while others provided a more detailed description of the type of occurrence. For the sake of this study, sporadic and permanent presence were considered together.

In order to obtain a continuous distribution of the species from the points, the toponym maps were processed with a Gaussian Kernel utilization distribution for each species separately. The Gaussian Kernel is commonly used in home range studies to map the area where an animal is likely to be at any given time (Worton 1987) expressed as density distribution. In home range estimation, the input points can be the locations of a single animal taken by GPS, to estimate individual home ranges, or the locations of all marked animals, to infer the distribution of the entire population (Clapp and Beck 2015). The 'core home range' is defined at the 90% or 95% threshold of the Kernel distribution and the 'total home range extent' at the 50% (Clapp and Beck 2015). In this study toponyms coordinates were used instead of animal locations to calculate two utilization distribution maps, one for each large carnivore considered. Using toponyms instead of locations of the whole populations, I expected that the 95% isopleth value (core home range) described the strongholds where the species were more abundant and therefore persisted longer in time of human persecution. Similarly, the 50% isopleths described the range of occurrence of the species when not disturbed by human presence. Cohen's Kappa coefficient (Smeeton 1985) was used to compare the maps of different isopleths of the density of place names with the historical distributions of bear and wolf (see Table 1), taken as ground truth. The Kappa value gives an idea of the spatial agreement of the maps and it can range from -1 to 1: negative value means no concordance, 0-0.20 slight, 0.21-0.40 fair, 0.41-0.60 moderate, 0.61-0.80 good and 0.8-1 excellent concordance.

All data were processed at a resolution of 1 km in the ETRS89 coordinate reference system using GRASS GIS 7.4 (GRASS Development Team 2012) for processing and QGIS 2.18 Las Palmas (QGIS Development Team 2015) for digitalization and layout (Preatoni et al. 2012; Rocchini and Neteler 2012).

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Table 1. Data used to assess the recolonisation and extinction patterns of large carnivores in Italy. LCI stands for Large Carnivore Initiative (http://www.lcie.org), PCN is the National Cartographic Portal of Italy created by Italian Ministry of the Environment (http://www.pcn.minambiente.it), OSM is Open Street Map (http://ww.osm.org) and ISTAT is the Italian National Institute of Statistics (http://datiopen.istat.it/).

Topic	Year	Type of map	Resolution	Type of information	Processing	Source
Toponyms	2011	Shapefile	250 m	Italian toponyms	Query	PCN
Toponyms	2018	Shapefile	5 m	Various type of locations	Query	OSM
Italian regions	2012	Shapefile	-	Boundaries of Italian regions	None	ISTAT
Bear	500 B.C	Image	100 km	Modelof presence	Digitalisation	Albrecht et. al 2017
Bear	1950	Shapefile	10 km	Presence of the species	None	Chapron et al. 2014
Bear	2011	Shapefile	10 km	Permanent and sporadic occurrence	None	Chapron et al. 2014
Bear	2011	Image	10 km	Permanent and sporadic occurrence	Digitalisation	LCI
Wolf	1900	Image	Not given	Presence of the species	Digitalisation	Randiet al. 2000
Wolf	1973	Image	Not given	Presence of the species	Digitalisation	Randiet al. 2000
Wolf	1985	Image	Not given	Presence of the species	Digitalisation	Randiet al. 2000
Wolf	1950	Shapefile	10 km	Presence of the species	None	Chapron et al. 2014
Wolf	2011	Shapefile	10 km	Permanent and sporadic occurrence	None	Chapron et al. 2014
Wolf	2015	Image	5 km	Permanent and sporadic occurrence	Digitalisation	Boitani et al. 2017

Results

The query of the PCN map returned about of 2700 records, of which 644 were considered meaningful for the names linked to brown bear. The same query on OSM instead yielded 623 records (valid 330) including names of places such as bars, restaurants and toy shops. The search of the words related to wolf on the PCN map returned 1636 records of which 1555 were valid, and only 423 from OSM. Due to their greater number, only the results from PCN map were further processed. Place names carrying obvious reference to those carnivores are located all across Italy, as shown in Fig. 1. The occasional toponyms in Sardinia actually described rock formations shaped like a bear or a wolf but, according to Cagnolaro et al. (1974), neither of these carnivores was ever present in this Island. To date I have not found evidence of bear/wolf-shaped formations in peninsular Italy, but as the species were present, the occasional rocks would not affect the density of the toponyms. Table 2 summarizes the results of the queries and of the classifications.

Some place names were found more than once at different places. Overall there were a total of 431 unique terms for bear and 1026 for the wolf: *Valle dell'orso* -valley of the bear- was the single commonest toponym with 18 occurrences while *Fosso del lupo* – ditch of the wolf- recurred 45 times. Most of the toponyms referred directly to natural features such as mountains, peaks, water sources or streams, but quite surprisingly, one of the most recurrent landmarks, named after both bears and wolves, was human settlements (Table 2); this category included castles, bridges, villages and isolated houses.

About the bear, the commonest place names referred to valleys, mountains and rivers but there were also 18 names mentioning caves and dens. In the case of the wolf, similarly, most frequent names referred to valleys and mountains but there were also 124 references to howling places *Cantalupo* – singing wolf-, an indication of the knowledge about the ecology and ethology of these carnivores.



Figure 1. Locations of the toponyms referring to the wolf (left) and the bear (right); the regional dialectal names are reported only when different from the Italian *lupo* -wolf- and *orso* -bear-.

Table 2. Number and percent of the toponyms related to the bear (N=644) and the wolf (N=1555) in Italy, classified according to the type of the most recurrent features named after the species and the occurrence of female, pejorative and endearment terms.

	Bea	r	Wolf			
	(N)	Percent (%)	(N)	Percent (%)		
Top feature	Valley (81)	17.5	Settlement (379)	17.9		
Second top feature	Settlement (71)	11.0	Ditch (137)	8.8		
Third top feature	Mount (62)	9.6	Valley (113)	7.3		
Female names	37	5.7	104	6.7		
Derogatory names	58	9.0	171	11.0		
Terms of Endearment	11	1.7	7	0.5		

Toponym locations were used to create two maps of density distribution, one for each species (Fig. 2): the density map for the bear name places had two big hot spots in the eastern Alps and in the Apennines, while the density of wolf names was high in various parts of the Italian peninsula. These maps were later reclassified according to the following thresholds: on top of the classic home range levels of 50%, 90% and 95%, also the standard quantiles of 25% and 75% were used. A new map was created for each level. All the density level maps were tested with the Kappa statistics against the available historical ranges for both species.



Figure 2. Density maps of the toponyms related to the brown bear (left) and to the wolf (right).

Table 3. Results of the Kappa statistics for each combination of historical ranges and thresholds of toponym density distribution. The cut off thresholds were chosen according to the HR theory and the pairing with historical distributions was decided according to the better fitting Kappa. Bear 2011 a is the distribution according to Chapron et al. (2014) and Bear 2011 b is the one from Large Carnivore Initiative. The highest level of accuracy is reported in bold. The area of the range of historical occurrence is also reported.

	Area (km ²)]	Kernel threshold	s	
Sp. time		25	50	75	90	95
Bear Roman times	186039	0.56	0.33	0.11	0.44	0.01
Bear 1950	2600	0.62	0.79	0.94	0.97	0.98
Bear 2011 a	11930	0.65	0.81	0.93	0.95	0.96
Bear 2011 b	36238	0.67	0.84	0.90	0.89	0.88
Wolf 1900	109513	0.39	0.68	0.67	0.67	0.62
Wolf 1950	9832	0.06	0.62	0.74	0.79	0.94
Wolf 1973	14195	0.08	0.64	0.76	0.81	0.93
Wolf 1985	27418	0.12	0.65	0.75	0.79	0.89
Wolf 2011	72423	0.27	0.66	0.72	0.73	0.75
Wolf 2015	89876	0.33	0.65	0.71	0.69	0.69

Table 3 reports the accuracy assessment for every combination of historical distributions and thresholds of toponym density using Kappa. Range contractions, that is smaller areas, are better classified by 90 and 90 thresholds, while large ranges better overlap with lower thresholds, as expected.

The maps of Figs 3 and 4 report the best matching pairs of historical ranges and density isopleths as illustrated in Table 3.

In agreement with the initial hypothesis, place names can be considered a proxy for locations: the different levels of the density in toponyms overlapped with the pattern of contraction and expansion of both species over time, average Kappa was 0.84 ± 0.5 (ranging from 0.67 to 0.95, 0.5 Standard Error). In particular, the smallest areas of occurrences for wolf and brown bears coincided with the highest densities of toponyms related to them.

Discussion

The best source for name places, both in terms of quantity and quality, proved to be the map of toponyms provided by the National Geo Portal for Italy. Once the locations of the place names of bears and wolf were retrieved, it was possible to analyse their spatial distribution and density as well as the recurrence and meaning of the names.

Distribution

The geographical location and spread of the toponyms allowed to test the hypothesis that name places are not only a legacy of a former presence but also a proxy for the density of the species.

In order to test it, the density of toponyms was calculated as in Cox et al. (2002). In addition, we further processed the results according to the home range theory and developed two series of maps of different densities that were used to identify hot spots of presence and to make comparisons with literature ranges, see Figs 2, 3 and 4.

The maps on the left of Fig. 3 depict the ranges of occurrence of the brown bear in Italy from Roman times to the present. Once widespread in the whole peninsula, the bear population declined over time due to habitat loss and direct persecution (Mustoni et al. 2003), and now it survives only in two separate populations. The maps on the right of Fig. 3 represent the best overlapping density maps of the toponym according to the Kappa statistics (see Table 3). The density of the place names accurately predicts the location and extent of the residual populations in the 1950s: the alpine in the north and the Marsican bear in the centre. Despite the map of Roman times, distribution has been obtained from a model with a coarse resolution; the overlap with the kernel is satisfactory (0.56), while for more recent and field derived maps, the matching with the toponym is excellent with Kappa always over 0.9. Presently, both populations are slowly recovering, following the afforestation trend that started after the 1950s (Tattoni et al. 2011; Ferretti et al. 2018) and the legal protection of the species. The alpine population is increasing faster than the southern one, thanks to a European reintroduction project (Tattoni et al. 2015; Tosi et al. 2015) and to the immigration of bears from Slovenia (Preatoni and Tattoni 2006). For the year 2011, are reported two sources that have a different spatial resolution and way of accounting for permanent and occasional presence (see Chapron et al. (2014) and LCI (https://www.lcie.org/). The one by Chapron and colleagues is more conservative than the one from LCI, but the toponyms still overlapped in accordance with both at different levels.

The maps on the left of Fig. 4 show the distribution of the wolf over time according to various sources and the maps on the right show the best matching threshold of the toponym density map (see Table 3). As for the bear, the maps of the density of the toponyms accurately predict the location and extent of the wolf population that shrunk from the beginning of the last century to a minimum in the 1970s, when it became extinct in the Alps and the northern part of the peninsula. In the 1970s, only isolated populations were found in the Apennines (Randi et al. 2000). After being granted legal protection in



Figure 3. Historical ranges of occurrence of the brown bear in Italy (maps on the left): the Roman time distribution was redrawn from Albrecht et al. (2017), 1950 and 2011 were downloaded from Chapron et al. (2014) while the other map of 2011 was adapted from the Large Carnivore Initiative 2018 www.lcie. org. The isopleths of the best matching density kernel calculated from the toponyms are reported in the maps on the right. The thresholds of the density kernel and the Kappa parameter of spatial concordance are reported for each pair of maps.



Figure 4. The maps on the left depict the historical ranges of occurrence of the wolf in Italy: the distributions in 1900, 1973 and 1985 were adapted from Randi et al. (2000) and the one in 2015 from Boitani et al. (2017). The isopleths of the best matching density kernel calculated from the toponyms are reported in the maps on the right. The thresholds of the density kernel and the Kappa parameter of overlapping are also reported for each pair of maps.

1981, the wolf population naturally recovered throughout Italy, almost to its 20th century status. The maps of 1950 are very similar to those of 1973 and they were omitted from Fig. 4. The main differences between the 1900 and the present distribution are in the western Alps, where the wolf is currently found and in Sicily, where the species is now absent but was present in the previous century instead. In the case of the wolf, the toponym derived maps and the distributions had good overlap with a 0.67 <Kappa <0.81.

The drivers for contraction and expansion of the wolf and the bear in Italy were both environmental and socio economic. What brought both species to the brink of extinction was direct persecution in addition to habitat loss. In fact, after being granted legal protection, the wolf population recovered to its 1900 status after just 40 years. For the bear, on the other hand, recovery is at a much lower pace. The ecology of the two species can explain the difference in the observed rate of recovery. The brown bear has a lower birth rate, females gave birth every second year and are mostly philopatric (Zedrosser et al. 2007) so even when surrounded by a suitable habitat the females tend to live near the home range of their mothers.

The results presented by Cox et al. (2002) reported an average 83% overlap between name place distribution for 17 species and their historical ranges, which is similar to what is found in this study, where the average Kappa is of 0.84. In the present work a higher Kappa (0.9) overlapped better in case of habitat reduction.

Perception of the species

Positive and negative connotation of place names are a legacy of the complex relationship between humans and large carnivores. Various natural features such as mountain tops, valleys and rivers have been named after these two mammals. However, some names clearly had a negative connotation, more rarely a positive one, while most of the times they were neutral.

Especially in the case of the wolf, nearly 11% of the names contained aggressive words that referred to the unconcealed wish for a dead or injured wolf. Toponyms such as *Lupara*, that indicate the place of the capture of the wolf (Calabrese 2015) and, later in time, the specific model of gun designed for wolf hunting, was found 87 times. *Caccialupo* -hunt the wolf- recurred 13 times and *Mazzalupo* -kill the wolf- 12 all around the country. Other expressions had a more regional connotation such as *Cecalupo* -blind the wolf- that occurred only in the region around Rome or *Scannalupi* -slay the wolves-present only on the island of Sicily. Competition for sheep, cattle and game species was harsh until 1950 when most of Italy relied on agriculture, and the desire to get rid of this predator was strong. Only a single place name directly expressed love towards the wolf: *Bacialupo*, literally meaning 'kiss the wolf', and six names refer to wolf pups.

Toponyms about bears suggested a slightly less negative association: only about 9% of them contained an explicit reference to capture or killing. Similarly to the wolf, the name *Orsara*- the place to hunt the bears- recurred 53 times throughout Italy, while *Mazzalorsa*, a combination of the words (*Am*)*mazza*-kill- and *l'orsa* – the female bear-occurred 4 times in the southern region of Puglia, and *Orsaccia* a pejorative term, just

once. Quite interestingly, the harmful terms always referred to the female bear, maybe perceived as more dangerous than the males because female bears can become very aggressive when defending their cubs. Overall, references to the female of the species were around 6% for both carnivores. The dozen names (2%) containing a direct reference to bear cubs were found only in north-west Italy; a direct expression of love or compassion was not very common for either the bear or the wolf.

Bears and wolf are indeed icons of wilderness (Tattoni et al. 2017a) and their names are still a popular choice for hotels and restaurants, a recognised index of their cultural value (Schirpke et al. 2018).

Conclusions

In this work I successfully applied the home range theory to the locations of toponyms for two large carnivores, and found a good overlap of place-names densities with extinction and recolonisation dynamics.

The semantic analysis of the names revealed a mixture of fascination with the wolf and bear, as well as fear of these animals, on the part of Italians in the past.

Such an exercise can raise public awareness about the past presence of the species on the Italian peninsula. The maps can be presented in discussions with stakeholders or during dissemination events to highlight the historical heritage of the territories and the cultural value of large carnivores. By analysing names, we can discover that the coexistence was not always peaceful and that large carnivores evoked awe and admiration but also fear. Acknowledging that the relationship was not easy in the past, but still predators were considered worth naming places after them, can help to understand the overall complexity of the issue.

Where people lost contact with large carnivores, they also abandoned traditional practices to protect herds and properties from them (D'Cruze et al. 2014) and they are not ready to implement necessary measures when the predators return. Traditional ecological knowledge fades in few generations if there is no day to day contact with the species or the environment in which the species are found (Tattoni et al. 2017b). However, toponyms last longer than human memories and are there to remind us of previous and not so remote times. The geographical analysis of name places may thus provide important information for species and habitat conservation or restoration, although its application is likely limited to large, charismatic species (Cox et al. 2002).

Nomen omen is a Latin idiomatic phrase that can be translated as: "destiny is in your name": Name place can explain your destiny, at least if you are a large carnivore.

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Supplementary material I

Figure S1. Relationship between the degree of accuracy (Kappa) and the area occupied by the species

Authors: Clara Tattoni

Data type: statistical data

- Explanation note: Relationship between the degree of accuracy (Kappa) and the area occupied by the species according to the literature at different thresholds of the density distribution with the regression line for each.
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RESEARCH ARTICLE



Distribution of Caulerpa taxifolia var. distichophylla (Sonder) Verlaque, Huisman & Procaccini in the Mediterranean Sea

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Abstract

The Non-Indigenous Species (NIS) *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman & Procaccini has been reported for the first time in the Mediterranean Sea along the coast of South Turkey. This NIS is actively expanding into the Eastern and Western Mediterranean Sea. In this paper, we present an overview of the current distribution of this alga in the Mediterranean Sea, based on relevant scientific publications, grey literature and personal observations. New records from the Sicilian coast (Italy) are also reported. *Caulerpa taxifolia* var. *distichophylla* was found over a wide range of environmental conditions (depth, light and substratum), suggesting a broad ecological plasticity of this alga which makes it a potential threat for the Mediterranean benthic communities. In this respect, artificial structures, often linked to harbours and maritime traffic, seem to provide suitable habitats for this NIS. Since maritime traffic is intense in the Mediterranean Sea, further expansion of *C. taxifolia* var. *distichophylla* in this region is to be expected. For this reason, it is very important to build up an overview on the current distribution of the species and its possible pattern of colonisation in relation to environmental conditions, as well as in view of future climate change scenarios.

Keywords

Non-Indigenous species (NIS), *Caulerpa taxifolia* var. *distichophylla*, Sicily coast, artificial marine infrastructures, Mediterranean Sea

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Introduction

The spread of Non-Indigenous Species (NIS, i.e. organisms introduced outside of their natural, past or present range and outside of their natural dispersal potential) has been pointed out as a major threat to biodiversity (Wallentinus and Nyberg 2007; Katsane-vakis et al. 2014; Vergés et al. 2016). NIS may become invasive (Invasive Alien Species "IAS") and may cause biodiversity loss and ecosystem service changes (Brunel et al. 2013; Giakoumi 2014; Vergés et al. 2014, 2016), thus representing a serious concern for nature conservation and economic activities (Occhipinti-Ambrogi and Galil 2010). In the Mediterranean, the number of recorded NIS has been currently reaching around 1000, of which 134 species are macrophytes (24 Chlorophyta, 79 Rhodophyta, 30 Ochrophyta and 1 Tracheophyta; Zenetos et al. 2012; Galil et al. 2015; Verlaque et al. 2015; Alós et al. 2016).

Amongst the NIS recorded in the Mediterranean Sea, *Caulerpa* taxa (*Caulerpa* cylindracea Sonder, *Caulerpa taxifolia* (M. Vahl) C. Agardh and *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman and Procaccini) have raised serious concern due to their potential or ascertained impact on the native communities (Boudouresque et al. 1995; Klein and Verlaque 2008; Katsanevakis et al. 2014).

Jongma et al. (2013) proposed the name *C. taxifolia* var. *distichophylla* for a gracile form of *C. taxifolia* reported in 2006 from the coasts of South Turkey (first Mediterranean record, Cevik et al. 2007) and one year later from Sicily (Cormaci and Furnari 2009; Meinesz et al. 2010). Morphologically, this form is very close to *Caulerpa distichophylla* Sonder, a species described from Western Australia, but differed from *C. taxifolia*. However, slight genetic differences observed between these two species led Jongma et al. (2013) to propose the new combination, which is currently accepted taxonomically (Guiry and Guiry 2019).

Later, *C. taxifolia* var. *distichophylla*, has been reported from other Sicilian sites (Musco et al. 2014; Antoci et al. 2015; Picciotto et al. 2016; Mannino and Balistreri 2017; Di Martino et al. 2018), Calabria, Sardinia (Di Martino et al. 2018), Cyprus (Çicek et al. 2013; Tsiamis et al. 2014; Aplikioti et al. 2016), Malta (Schembri et al. 2015), Rhodes Island (Aplikioti et al. 2016), Lebanon (Bitar et al. 2017), Libya (Shakman et al. 2017) and Tunisia (Chartosia et al. 2018) (for details on localities see Fig. 1 and Table 1).

This invasive alien taxon, whose plausible pathway of introduction and spread is maritime traffic, has been pointed out as a potential threat for the indigenous communities but also for fishing activities (Jongma et al. 2013; Musco et al. 2014) and as potentially invasive by Aplikioti et al. (2016).

In the Mediterranean, maritime traffic plays an important role in the introduction and spread of NIS (Katsanevakis et al. 2014). The fact that many colonised areas are near harbours and exposed to human activities (e.g. shipping, tourism, fishing), would support this hypothesis (Mannino and Balistreri 2017). Since knowledge of distribution and spread dynamics of NIS within the Mediterranean Sea is of great importance, for management and conservation purposes as well as in view of future climate change scenarios, the aim of the present paper is to draw the current distribution and spread



Figure 1. Map showing countries in the Mediterranean Sea where *Caulerpa taxifolia* var. *distichophylla* has been recorded (see Table 1 for localities and detailed references).

dynamics of *C. taxifolia* var. *distichophylla* into the Mediterranean Sea and to provide additional records from the Sicilian coasts (North-Western Mediterranean Sea), together with some environmental and biological variables.

Materials and methods

Field surveys were carried out (summer 2015 and 2017) by the authors in six localities along the coast of Sicily (North-western Mediterranean) (see Fig. 2). In particular, two sites were located along the Northern coast: Termini Imerese (PA, 2015) and Cefalù (PA, 2017) and four along the southern coast: Isola delle Correnti (SR, 2015), Portopalo di Capo Passero (SR, 2015), Punta delle Formiche-Pachino (SR, 2015) and Concerie-Pachino (SR, 2015).

At each site, specimens (n = 20) of the alga were collected by snorkelling, at a depth of 0-10 m. Specimens were identified in the laboratory as *C. taxifolia* var. *distichophylla* on the basis of morphological characters (stolon, fronds, pinnules, rhizoidal pillars, midrib) used by Jongma et al. (2013) to characterise specimens from Sicily. Moreover, some environmental (depth, substrate) and biological variables (percentage cover) were registered. Depth was measured using a waterproof watch. Different classes of sub-

Country	Locality	Substrate	Depth (m)	Coverage level	Benthic assemblage	References
Turkey	Gulf of Iskenderun	silted sand	11	m.d.	m.d.	Cevik et al. (2007)
Italy	Punta Braccetto	rock	0.5–20	m.d.	m.d.	Cormaci and Furnari (2009)
	Capo Passero, Isola delle Correnti, Punta Braccetto	rock	m.d.	m.d.	m.d.	Meinesz et al. (2010)
	Punta Braccetto	rock	0.5-20	m.d.	m.d.	Jongma et al. (2013)
Turkey	Kas, Antalya, Gulf of Iskenderun	m.d.	m.d.	m.d.	m.d.	Jongma et al. (2013)
Cyprus	Agios Philon Church Bay, Dipkarpaz	rock	6–8	m.d.	Cystoseria spp., Posidonia oceanica	Çicek et al. (2013)
	Cavo Greco, Famagusta	rock	m.d.	m.d.	m.d.	Tsiamis et al. (2014)
Italy	Sant'Ambrogio, Donnalucata, Ragusa, Punta Secca, Torre di Mezzo, Punta Braccetto, Marina di Torre Salsa	dead matte, sand with pebbles, cobbles and boulders, rock	0–5	from < 10 to > 50%	Caulerpa cylindracea, Cymodocea nodosa, Posidonia oceanica, macroalgae	Musco et al. (2014)
Malta	White Rocks, Exiles in Sliema	rock and sediment	3–15	patches from 0.35 × 0.35 m to 22.0 × 4.0 m	Posidonia oceanica	Schembri et al. (2015)
Italy	Isola delle Correnti, Foce Fiume Irminio, Punta Braccetto, Marina di Acate, Malerba, Realmonte	dead matte, sand, sabellaria	3–9	from 10 to 5584 filloid*m ⁻²	Macroalgae, <i>Posidonia oceanica</i> , Sabellaria, <i>C.</i> <i>cylindracea</i>	Antoci et al. (2015)
	Termini Imerese, Portopalo di Capo Passero, Isola delle Correnti	rock, sand, shipwreck	1–10	from 1 to 50% and > 50%	Cymodocea nodosa	Present study (2015)
Cyprus	Cavo Greco, Agios Philon Church Bay, Rizokarpaso (Dipkarpaz), Sunrise Bay	biogenic sand, mud, biogenic hard substrate	< 1, 22, 34, 42, 48	99–100%	Caulerpa cylindracea, Caulerpa prolifera, Codium bursa, Cymodocea nodosa, Halophila stipulacea	Aplikioti et al. (2016)
Rhodes Island (Greece)	Lindos Bay, Charaki Bay, Karakonero Bay, Lahania	sand, sand/ mud, mud, rock, pebbles/shells	9–18, 20, 35, 50, 100	99–100%	m.d.	Aplikioti et al. (2016)
Italy	San Saba- Acqualadrone- Tono	sand	3–6	from < 8 to 26%	Halophila stipulacea, Penicillus capitatus, Posidonia oceanica	Picciotto et al. (2016)
Lebanon	El Madfoun and Byblos	sand and gravels	16-48	m.d.	m.d.	Bitar et al. (2017)
Libya	Tripoli	sand	m.d.	m.d.	Seagrass meadow	Shakman et al. (2017)
Italy	Termini Imerese	sand	9–10	from 1 to 50% and > 50%	Cymodocea nodosa	Mannino and Balistreri (2017)
	Cefalù, Punta delle Formiche-Pachino and Concerie-Pachino	sand, rock	2–5	from 20 to 50% and > 50%	Posidonia oceanica	Present study (2017)
Tunisia	Alataya Harbour, Djerba,Tabarka	sand, rock, dead matte	0.2–2	m.d.	Posidonia oceanica	Chartosia et al. (2018)
Italy	Stagnone di Marsala, Terrauzza Bay, Brucoli Bay, Augusta Harbour, Vendicari Natural Reserve, Scala dei Turchi Beach, Scilla (Calabria), Cagliari (Sardegna)	dead matte, sand, rock	0-4	m.d.	Cymodocea nodosa, Posidonia oceanica	Di Martino et al. (2018)

Table 1. Known sites of occurrence of *Caulerpa taxifolia* var. *distichophylla* in the Mediterranean Sea.

m.d.: missing data



Figure 2. Map showing localities surveyed in the present study.

strate were examined: natural (rock, sand, sand and rock) or both natural and artificial (sand, rock and shipwreck). The percentage cover was visually estimated (*in situ* and by using photographs of the frames) by placing a 20×20 cm frame (three replicates) (Mangialajo et al. 2008) and three classes were considered: 1 (cover < 20% and > 1%), 2 (cover < 50% and > 20%) and 3 (cover > 50%).

All the relevant publications, grey literature and reports dealing with *C. taxi-folia* var. *distichophylla* in the Mediterranean, from its first record in the area and updated till 2018, were also searched and analysed. A search, based on the following string: Caulerpa AND taxifolia AND "var. distichophylla" AND Mediterranean*, was performed using standard scientific databases (Scopus, Web of Science) (Marrocco et al. 2019).

Results

Field surveys

During the surveys, three new records of *C. taxifolia* var. *distichophylla* have been registered: Concerie-Pachino and Punta delle Formiche-Pachino, located along the southern coast and Cefalù located along the Northern coast. The alga was growing on both natural (mainly on rock) and artificial substrates, from 1 to 10 m depth (mainly in shallow waters). In all sites, only sterile specimens were found. We report below detailed information for each surveyed site.

Concerie-Pachino: the alga (fronds about 10 cm long) was found in shallow waters (at a depth of about 3 m) both on rocky substrate, forming patches of class 2 or 3 and on sandy substrate, forming patches of class 2.

Punta delle Formiche-Pachino: the alga (fronds not exceeding 10 cm in length) was recorded on rocky substrate in very shallow waters (at a depth of about 2 m), forming patches of class 2 or 3.

Isola delle Correnti (Figs 3A–D): the alga was found in shallow waters (at a depth of about 3 m and 300 m distant from the coastline) flourishing on a shipwreck, a boat sunk about 30 years ago on sandy substrate. Rocky and sandy substrates were both present around the shipwreck, but the alga was present only on rocky substrate. On the external surfaces of the shipwreck, *C. taxifolia* var. *distichophylla* (erect fronds not exceeding 5 cm in length) formed patches of class 1 or 2. On the internal surfaces of the shipwreck, the alga (erect fronds about 10–15 cm long) formed patches of class 1 or 3.

Portopalo di Capo Passero: the alga, with fronds not exceeding 10 cm in length, settled on rocky substrate in very shallow waters (at a depth of about 1-2 m), forming patches of class 2.

Cefalù: the alga, with fronds 5–10 cm long, was found at a depth of about 4–5 m on rocky substrate and at the base of *Posidonia oceanica* (L.) Delile, forming patches of class 2.

Termini Imerese: the alga, with fronds 5–10 cm long, was found on sandy substrate at a depth of about 9–10 m, forming patches of class 1 along the borders of a *Cymodocea nodosa* (Ucria) Ascherson meadow (Fig. 3E–F).

Literature data

The analysis of literature data also highlighted that *C. taxifolia* var. *distichophylla* is able to thrive under a wide range of environmental conditions (see Table 1 for details on records). It grows mainly in shallow waters, even though it was found from the surface down to 100 m depth. It is mainly found on sand, but it can also grow on biogenic substrates, calcareous algae, pebbles, cobbles, sand, rock, mud and artificial substrates. It can grow both under low and high light conditions, though in shaded conditions, it is more abundant and with longer fronds. It occurs alone but also intermingled with other NIS (*C. cylindracea* and *Halophila stipulacea* (Forsskål) Ascherson) or native macroalgae, on dead matte of *P. oceanica* and *C. nodosa*, as well as along the borders or in vicinity of *P. oceanica* meadows. The level of colonisation ranged from sparse individuals to patches (from 0.35×0.35 m to 22.0×4.0 m), the number of filloid ranged from 10 to 5584 m² and the substratum cover (%) ranged from 8% to 100%.



Figure 3. *Caulerpa taxifolia* var. *distichophylla* **A–D** patches on the shipwreck at Isola delle Correnti (photos by Francesco Cicero) **E–F** small patches at Termini Imerese (photos by Marco Toccaceli).

Discussion

Though there is a certain limitation in the collection of data by snorkelling, this technique allows the gathering of useful data and information on NIS, mainly in shallow waters (Imbert 2014). Field surveys confirmed the presence of *C. taxifolia* var. *distichophylla* in sites where it was previously recorded (Mannino and Balistreri 2017), but also allowed us to register new populations both in the southern and in the northern coast of Sicily, suggesting the spread of this alga is an on-going process along the Sicilian coasts. Along the southern coast, it was recorded in very shallow waters (between 1 and 3 m), whereas in the northern coast, it was found both in shallow and deeper waters (between 4 and 10 m). In reduced light conditions (e.g. on the inside surfaces of the shipwreck), the alga had longer fronds.

Moreover, it seems to prefer rocky and artificial substrates (patches of class 3) more than sandy bottoms. In particular, the alga really flourished on the structures of the shipwreck. Caulerpa taxifolia var. distichophylla, as well as the congeneric C. cylindracea, seem to grow well on artificial structures (e.g. shipwrecks, present study and Ragonese and Rizzo 2017), which may provide suitable habitat for marine NIS but also enhance their further spread, by functioning either as stepping stones or even corridors for their expansion (e.g. Bulleri and Airoldi 2005; Ruiz et al. 2009; McNeill et al. 2010; Mineur et al. 2012). In this respect, artificial structures could act as sentinel places for monitoring the appearance of new NIS (Ruiz et al. 2009; Peirano 2013). The analysis of literature data highlighted how, in colonised areas, C. taxifolia var. distichophylla is able to adapt well to different environmental conditions (e.g. light, depth, substrate) more than in native areas where it is found on sand up to 6 m depth (Womersley 1984). The alga is also able to grow in deeper waters than the congeneric *C. cylindracea* (Klein & Verlaque, 2008); indeed it was found to at least 100 m depth, even though the presence at 100 m depth still needs to be confirmed (Aplikioti et al. 2016). Certainly, the ability to adapt well to different environmental conditions makes C. taxifolia var. distichophylla a potential threat for the indigenous communities (Musco et al. 2014; Aplikioti et al. 2016). However, its impact on Mediterranean habitats and associated communities (i.e. P. oceanica, hard bottoms) has not yet been ascertained (Cevik et al. 2012; Musco et al. 2014, 2015).

The recent records of C. taxifolia var. distichophylla along the Sicilian coasts, in Rhodes Island (Aplikioti et al. 2016), Lebanon (Bitar et al. 2017), Libya (Shakman et al. 2017), Tunisia, Sardinia and southern coast of Italy (Chartosia et al. 2018; Di Martino et al. 2018) confirm that C. taxifolia var. distichophylla is actively spreading into the Mediterranean Sea, expanding beyond its northern and western limit (Musco et al. 2014). Sicilian populations of C. taxifolia var. distichophylla, probably entered independently from the Turkish one. The regular and intense maritime traffic between Sicily and other Mediterranean countries could be responsible for the introduction of this alga along the Sicilian coasts but also for a secondary introduction from Sicily to other regions such as Malta, Sardinia and Calabria (Schembri et al. 2015; Di Martino et al. 2018). Since maritime traffic can produce a constant spill-over of new invaders into surrounding areas, Sicily and Turkey could have played and are still playing an important role as receiver, transit and probably sources for secondary dispersal of NIS, respectively within the Eastern and Western basin of the Mediterranean Sea. Therefore, knowledge of spread dynamics of NIS in these areas is of great importance for all the Mediterranean Sea, as well as for management purposes.

Sicily and circum-Sicilian Islands are inhabited by a rich biota (e.g. Domina et al. 2018) and have a high number of Marine Protected Areas (MPAs). As a consequence of their geographic position and by virtue of the intense maritime traffic volumes cross-

ing the region, they are particularly vulnerable to biological marine invasions (Occhipinti-Ambrogi et al. 2011a, b; Coll et al. 2012; Katsanevakis et al. 2014; Mannino et al. 2014, 2015, 2017, 2018; Mannino and Balistreri 2017). Therefore, this area should be regularly and carefully monitored.

Moreover, a warmer and drier Mediterranean region, as forecast for the 21^{st} century (Ben Rais Lasram et al. 2010), will certainly facilitate the further expansion of *C. taxifolia* var. *distichophylla*. Its occurrence, in association with tropical-subtropical macrophytes (e.g. *H. stipulacea* and *Penicillus capitatus* Lamarck), suggests that a reorganisation of benthic communities as a consequence of global change is already underway within the Mediterranean Sea (Evagelopoulos et al. 2008; Picciotto et al. 2016).

For a better understanding of the invasive potential and spread dynamics of NIS, a quick sighting of any newly colonised area (Klein and Verlaque 2008), together with good knowledge of environmental and biological factors enhancing their spread, is fundamental. Therefore, the establishment of regular monitoring programmes, including public awareness campaigns, citizen science initiatives and online databases or networks, are necessary in areas at risk, such as Sicilian coasts (included MPAs), particularly areas located in proximity to ports, marinas and transitional waters (e.g. Orfanidis et al. 2007), in order to increase knowledge on distribution and spread dynamics of IAS (Mannino and Balistreri 2018). Moreover, the identification of threatening NIS at the earliest stages of their introduction increases the chances for effective control (Bieler et al. 2017).

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RESPONSE



Megafire effects on spotted owls: elucidation of a growing threat and a response to Hanson et al. (2018)

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Abstract

The extent to which wildfire adversely affects spotted owls (Strix occidentalis) is a key consideration for ecosystem restoration efforts in seasonally dry forests of the western United States. Recently, Jones et al. (2016) demonstrated that the 2014 King Fire (a "megafire") adversely affected a population of individuallymarked California spotted owls (S. o. occidentalis) monitored as part of a long-term demographic study in the Sierra Nevada, California, USA because territory occupancy declined substantially at territories burned at high-severity and GPS-tagged spotted owls avoided large patches of high-severity fire. Hanson et al. (2018) attempted to reassess changes in territory occupancy of the Jones et al. (2016) study population and claimed that occupancy declined as a result of post-fire salvage logging not fire per se and suggested that the avoidance of GPS-marked owls from areas that burned at high-severity was due to post-fire logging rather than a response to high-severity fire. Here, we demonstrate that Hanson et al. (2018) used erroneous data, inadequate statistical analyses and faulty inferences to reach their conclusion that the King Fire did not affect spotted owls and, more broadly, that large, high-severity fires do not pose risks to spotted owls in western North American dry forest ecosystems. We also provide further evidence indicating that the King Fire exerted a clear and significant negative effect on our marked study population of spotted owls. Collectively, the additional evidence presented here and in Jones et al. (2016) suggests that large, high-severity fires can pose a threat to spotted owls and that restoration of natural low- to mixed-severity frequent fire regimes would likely benefit both old-forest species and dry forest ecosystems in this era of climate change. Meeting these dual objectives of species conservation and forest restoration will be complex but it is made more challenging by faulty science that does not acknowledge the full range of wildfire effects on spotted owls.

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Introduction

The spotted owl (Strix occidentalis) has become an icon of conservation in North America because of conflicts amongst citizens, conservation groups, the timber industry, natural resource agencies and politicians arising over the best way to protect its economically valuable old-forest habitats (Simberloff 1987, Gutiérrez et al. 1995; Gutiérrez 2015). This basic conflict has expanded in recent years to include disputes that weigh the potential degradation of owl habitat from restoration projects in dry forest ecosystems that seek to reduce severe fire risk (e.g. logging, thinning, prescribed burning) against the potential risk posed to owl habitat by the increasing number of large, high-severity fires (Lehmkuhl et al. 2007, 2015; Collins et al. 2010; Tempel et al. 2014, 2015, 2016). A second element of this conflict relates to the nature of current and historical conditions and fire regimes. On the one hand, much research has shown that tree densities are higher now than they were prior to the beginning of fire suppression efforts in the early 20th century (e.g. Collins et al. 2017; Hagmann et al. 2017; Safford and Stevens 2017). Under this paradigm, lower tree densities and fuel loadings in historical dry forests were maintained by a frequent low- to moderate-severity fire regime (including smaller patches of high-severity fire), but modern fire suppression has allowed an increase in tree densities and fuel loadings that have, in turn, led to an increase in the frequency of large, high-severity fires (e.g. Calkin et al. 2005; North et al. 2015; Steel et al. 2015; Stevens et al. 2017). On the other hand, some researchers have suggested that larger patches of high-severity fire were relatively common in historical post-fire landscapes in dry forest types (Hanson et al. 2009, Williams and Baker 2012, Hanson and Odion 2014, Odion et al. 2014, Baker and Hanson 2017), although the validity of inferences from these studies has been contested (Spies et al. 2010, Fulé et al. 2014, Safford et al. 2015, Stevens et al. 2016, Hagmann et al. 2018). Hence, under the first paradigm, fuels reduction and forest restoration treatments are needed to reduce tree density and return forests ecosystems to the lower-severity fire regimes that were historically typical. Under the second paradigm, fuels reduction and forest restoration treatments are not necessary because current fire regimes in dry forests are consistent with historical ecosystem processes. The second paradigm also predicts that owls should not be negatively impacted by large, high-severity fires. However, if they are negatively impacted by large, high-severity fires, then it lends some support to the need for forest restoration. Therefore, knowing how high-severity fires affect spotted owls is pivotal to the management of dry forests in western North America.

There are two important questions for conservation scientists to address: (1) do management actions, intended to decrease risk of high-severity fire by reducing tree densities and surface fuels (e.g. thinning, prescribed fire), cause more or less harm to spotted owls than high-severity fire itself; and (2) how do owls respond to large, high-severity fires given they appear to be adapted, at least, to low- to moderate-severity fire regimes? Regarding the first question, we know that owls can be negatively impacted by restoration efforts in the short-term (Ager et al. 2007, Stephens et al. 2014, Tempel et al. 2014, 2015, 2016), but we do not know the extent to which these short-term

impacts might mitigate loss of habitat or other impacts caused by high-severity fires. Regarding the second question, while there is unanimous empirical support that predominately low-severity fires have little negative impact on owls (Bond et al. 2002, Bond 2016, Ganey et al. 2017), there are two general alternative findings about the effect of large, high-severity fires on owls: neutral/beneficial effects (e.g. Bond et al. 2009, 2016; Lee et al. 2012; Lee and Bond 2015; Hanson et al. 2018) and negative effects (Comfort et al. 2016; Jones et al. 2016; Eyes et al. 2017; Ganey et al. 2017; Rockweit et al. 2017) (see also below the section "The science of spotted owls and fire"). Determining which of these results is correct will influence how forest restoration proceeds within the range of the spotted owl.

A paper published recently in *Nature Conservation* (Hanson et al. 2018) attempted to reverse the growing scientific consensus that large, high-severity fires can negatively impact spotted owl populations (Comfort et al. 2016, Jones et al. 2016, Eyes et al. 2017, Ganey et al. 2017, Rockweit et al. 2017), claiming instead that post-fire salvage logging-not high-severity fire-poses the key threat to owls in post-fire landscapes. While the analysis performed by Hanson et al. (2018) included data from several recent large fires, a large portion of the discussion section of Hanson et al. (2018) was devoted to re-interpreting and criticising our study published in *Frontiers* in Ecology and the Environment (Jones et al. 2016). Jones et al. (2016) demonstrated unambiguous negative effects of a large (~40,000 ha) high-severity fire, the 2014 King Fire, on a study population of spotted owls in the central Sierra Nevada, CA. This large fire occurred partly within the boundary of our long-term, demographic study area containing individually-marked California spotted owls. In addition, we (Jones et al. 2016) found no effect of salvage logging on the owls, but Hanson et al. (2018) claimed that the negative effects of the King Fire on spotted owls was due to salvage logging, not severe fire. Therefore, we developed this paper for two reasons. First, the conclusions reached by Hanson et al. (2018) lacked scientific merit because their inferences were negatively influenced by factual errors (owing to a lack of understanding of our data and our study population), errors in their data and inadequate statistical approaches. Second, there could be negative repercussions for species conservation, forest restoration and fire management in the western United States if the conclusions of Hanson et al. (2018) are not corrected. We begin by contextualising the Hanson et al. (2018) and Jones et al. (2016) papers within the current state of science of spotted owls and fire and then proceed to document the inaccuracies and mistakes in Hanson et al. (2018).

The science of spotted owls and fire

Spotted owls are adapted to low- to moderate-severity fire regimes as evidenced by no research revealing a negative response to these types of fires (Gutiérrez et al. 1995, 2017; Bond et al. 2002, Bond 2016, Ganey et al. 2017). Yet, literature reviews have revealed that spotted owls show a wider range of responses to highseverity fire (Bond 2016, Ganey et al. 2017, Lee 2018). One research group has inferred generally neutral or positive effects of high-severity fire on occupancy rates and owl foraging behaviour (Bond et al. 2009, 2016, Lee et al. 2012, 2013; Lee and Bond 2015, Lee 2018). In contrast, four other research groups, working independently of each other, have reported negative effects of high-severity fire on both owl population dynamics and foraging behaviour (Comfort et al. 2016, Jones et al. 2016; Eyes et al. 2017, Rockweit et al. 2017). Thus, a disparity exists that requires resolution because conservation decisions to restore forests or protect owl habitat are somewhat dependent on knowing the manner in which owls are expected to respond to high-severity fire.

We offer two possible explanations for the above contrasting results. First, variation in results from field studies can often be explained by differences amongst study systems and unique patterns and intensities of wildfires. For example, we know that the Rim Fire studied by Lee and Bond (2015) showed a different pattern of burning than the King Fire we studied (Jones et al. 2016); the former exhibiting more variability in intensity and pattern of burning and the latter being more uniformly intense with very large patches of high-severity burn (e.g. one contiguous patch was >13,500 ha) (see Stevens et al. 2017). Thus, it is logical to expect fires having different patterns of burn severity to affect a species differently.

Second, study methods influence data quality. We had an extensive individual history of owls affected by the King Fire because we had colour-marked and resighted birds in our study area for the 22 years preceding (1993-2014) as well as annually after the King Fire. Knowing the identity of individuals allowed us to associate individuals with places and, more importantly, allowed us to exclude false positive detections in survey/location histories of birds (Berigan et al. 2018). Interestingly, studies by Lee et al. (2012, 2013), Lee and Bond (2015) and Hanson et al. (2018) on occupancy dynamics of spotted owls showed no negative effects of high-severity fire but relied primarily on night-time detections of unmarked owls to assign the occupancy status, which suggests false positive detections could have been included in analysis (Berigan et al. 2018). It has been shown that even low rates of false positive detections result in positive biases that inflate occupancy rate estimates (Royle and Link 2006, Miller et al. 2011, Sutherland et al. 2013). We also knew from GPS-tagbased studies of spotted owls that owls frequently move amongst unoccupied (and sometimes occupied) territories (Berigan et al. 2018, Blakey et al. 2019). Therefore, we were able to exclude false positive detections from our owl detection database because we knew which owls were present at a given historical territory owing to our observation of their colour bands, both before and after the King Fire. In contrast, Hanson et al. (2018) and others (e.g. Lee and Bond 2015) were unable to do this because they relied on night-time observations of unmarked owls collected by others or otherwise did not have access to survey metadata that contained information regarding individual owl identity (see below). Therefore, we believe the quality of data in Jones et al. (2016) was higher than the data used by Hanson et al. (2018) in their re-analysis.

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Jones et al. (2016) tested the effects of high-severity fire on owls using a "natural" Before-After Control-Impact (BACI) design

Hanson et al. (2018:101) criticise a central finding of a decline in owl occupancy following the King Fire, reported by Jones et al. (2016), as "not sound" while also providing alternative explanations for other results in Jones et al. (2016). So we here summarise the salient points of Jones et al. (2016), which we follow with an exposition of the errors in Hanson et al. (2018) that led to their spurious conclusions. The 2014 King Fire partially occurred within the 23-year Eldorado spotted owl demographic study used by Jones et al. (2016), but the fire only impacted about half of the study area. Thus, the King Fire created an ideal structure for a natural Before-After Control-Impact study (BACI; Popescu et al. 2012) in which half the area was "treated" by fire and the other half was not "treated." Moreover, we had over two decades of pre-fire data, colour-marked individual owls and temporally consistent, standardised robust (i.e. repeated surveys within and amongst years) survey data for the owls that were either potentially affected or not affected by the King Fire (Jones et al. 2016). Due to the long-standing conflicts surrounding the conservation of the spotted owl (Gutiérrez et al. 1995, Gutiérrez 2015), these survey methods have been peer-reviewed many times (e.g. Franklin et al. 2004, Blakesley et al. 2010).

The King Fire occurred in September and October 2014, but Jones et al. (2016) began assessing effects of the fire on owls the following spring breeding season (2015). Of the 45 long-term territories – defined as 1100-m radius circles centred on nests and roosts - monitored in the above-described density study area, 14 burned with > 50% high-severity fire over the entire territory, 16 burned with < 50% high-severity fire over the entire territory and 15 experienced no fire. We assessed the potential for fire effects on spotted owls separately from potential effects of salvage logging in our modelling, but only a relatively small amount of salvage logging occurred on private land prior to the conclusion of our owl surveys at the end of the 2015 breeding season (see also below for specific comments on potential effects of salvage logging). Moreover, our survey design, with multiple surveys conducted per territory every year, allowed for the rigorous modelling of detection probabilities within a multi-season occupancy modelling framework (MacKenzie et al. 2003). Finally, at the same time territory occupancy was being assessed in 2015, we deployed nine GPS tags on spotted owls that had persisted around the periphery of the large patch of forest burned at high-severity to characterise how fire affected patterns of owl foraging habitat selection.

Our key findings in Jones et al. (2016) were:

- (1) The likelihood of a territory that was *occupied* in the breeding season prior to the King Fire (i.e. 2014) becoming extinct the year following the fire (i.e. 2015) was strongly and positively associated with the proportion of the territory that burned at high severity.
- (2) Seven of eight territories that were *occupied* during the breeding season prior to the King Fire (i.e. 2014) and that also experienced > 50% high severity fire became

"extinct" after the fire (i.e. 2015). The estimated territory extinction rate at highseverely-burned territories after the fire (0.88) was ~7 times greater than average annual extinction rates (0.12) for the same territories or any other group of territories–*well* beyond the range of variability estimated for the previous 22 years (Tempel et al. 2016).

- (3) In some cases, both high-severity fire and salvage logging occurred within owl territories, but high-severity fire was predominant in its spatial extent by an order of magnitude. At 1100 m and 1500 m scales, the area affected by high-severity fire was ~17 and ~12 times greater, on average, than salvage logging (where salvage logging actually occurred). We (Jones et al. 2016) explicitly modelled effects of salvage logging, which explained negligible variation; we therefore inferred salvage logging to be an uninformative parameter (*sensu* Arnold 2010).
- (4) None of the 6 territories that were *unoccupied* during the breeding season prior to the King Fire (i.e. 2014) and experienced > 50% high severity fire was recolonised (i.e. became occupied) by new birds in 2015.
- (5) Collectively, (2) and (4) resulted in only 1 of 14 territories that experienced > 50% high-severity fire remaining occupied the year after the King Fire. The single occupied territory contained a pair of owls (although a "turnover" occurred with a new male pairing with the same female who was present pre-fire) that shifted their activity centre > 1,300 m to the east from within their severely-burned historical nest stand into a stand that experienced predominately low-severity fire.
- (6) The King Fire resulted in the largest negative rate of change in population occupancy (λ) observed for a single year (22% decline from the previous year) in territory occupancy over the 23-year Eldorado study.
- (7) Three instances of breeding dispersal by individually-marked owls out of the highseverity-burned territories and into the surrounding and low- to moderate- severity burned landscape were documented, even though breeding dispersal in California spotted owls is relatively rare (Gutiérrez et al. 2011).
- (8) We observed one apparent adult mortality associated with the King Fire, as evidenced by our finding of the scorched remains of an owl carcass with its United States Geological Survey (federal government) aluminium locking leg band near a high-severity-burned nest site. Band numbers corresponded with an individual that we observed to be alive at this site several weeks prior to the King Fire.
- (9) GPS-tagged owls persisted in less severely burned territories around the large high-severity burned patch, but showed strong avoidance of the large high-severity burned area for foraging (even when the central place foraging behaviour of spotted owls was accounted for; see below).

Collectively, these results indicated that the King Fire had a major negative effect on both spotted owl habitat and the local spotted owl population. Moreover, the 13% decline in absolute territory occupancy (22% rate of change in occupancy) from 2014 to 2015 in the Eldorado density study area likely did not represent the full impact of the King Fire to the local population because territories that experienced large amounts
of high-severity fire have likely been rendered unsuitable to spotted owls for nesting and roosting for decades. The loss of territories, then, will reduce carrying capacity and will limit the growth of the population. In support of this hypothesis, all of these unoccupied territories have remained unoccupied in 2016, 2017 and 2018 (M. Z. Peery, *unpublished data*).

Hanson et al. (2018): error-fraught criticisms of Jones et al. (2016)

Given the results published by Jones et al. (2016), Hanson et al. (2018) attempted to compare the relative effects of high-severity fire vs. salvage logging on occupancy rates of California spotted owl territories. While this study included data from eight large fires in California occurring from 2002–2015, a key conclusion was that the 2014 King Fire did not negatively impact California spotted owls as inferred by Jones et al. (2016). Instead, Hanson et al. (2018:101) argued that the observed occupancy declines and high extinction rates in severely burned spotted owl territories reported by Jones et al. (2016) were due to post-fire salvage logging, not high-severity fire, stating that:

"...the conclusion by Jones et al. (2016), that the King fire caused the loss of occupancy in these sites, is not sound."

We do not argue against Hanson et al.'s point that salvage logging *can* negatively impact spotted owls, particularly when such logging occurs in forests used by owls (e.g. fires burning in a mosaic pattern often leave areas suitable for owl use). In the case of the King Fire, however, the independent effect of high-severity fire on spotted owls was unambiguous. The claim made by Hanson et al. (2018) that declines in owl occupancy and foraging in forests burned at high-severity by the King Fire were the result of salvage logging, not high-severity fire, is without scientific merit and is the result of clear factual errors and erroneous inferences. Below, we describe seven issues, focusing on Hanson et al.'s inferences as they relate to the findings of Jones et al. (2016).

(1) Hanson et al. excluded the most severely-burned spotted owl sites from their analysis. A key reason why Jones et al. (2016) made strong inferences regarding the effects of severe fire on spotted owls is because they documented extinction in 7 of 8 territories that burned at high severity across > 50% of their territory area (62–99% high severity) that were occupied pre-fire (PLA0050, PLA0067, ELD0058, PLA0113, PLA0039, ELD0057, PLA0065 [see Suppl. material 1: Figure S1 for PLA 0113, Suppl. material 2: Figure S2 for PLA 0065 and Suppl. material 3–6: Figures S3–S6 for general views of the extent and relative severity of the King Fire] – these are unique codes corresponding to United States Forest Service [USFS]-delineated spotted owl management units). Of these seven territories, Hanson et al. (2018: 97) deliberately excluded the four most severely burned (91–99% high severity) from their analysis (i.e. PLA0050, PLA0067, PLA0113 and PLA0065) claiming, it appears, that including sites that burned at > 80% high severity fire would have apparently created an "analytical problem" for their analysis – "*Conversely, the effects of post-fire logging*

were not analysed for sites with > 80% high-severity fire because nearly all of these sites have $\geq 5\%$ post-fire logging and there was not a sufficient number of such sites with \geq 5% post-fire logging for the analysis" – but we do not understand the rationale because their decision effectively removed from analysis many territories most likely to show a negative effect of high-severity fire. Additionally, using categorical rather than continuous variables (as we did in addition to categorical covariates) to represent fire and salvage logging effects provides less analytical power (Cottingham et al. 2005). Finally, from an ecological perspective, it is arbitrary to subdivide territories that burned at > 50% high-severity into two groups (50-80% and > 80%) and subsequently eliminate the > 80% category, as Hanson et al. did. By doing so, they deliberately eliminated from their analysis those territories most extensively affected by high-severity fire and, therefore, those territories which would most likely demonstrate high-severity fire effects on spotted owl territory occupancy. Thus, Hanson et al. (2018) included only three of the seven sites (ELD0058, PLA0039 and ELD0057) that actually became unoccupied ("went extinct") after the King Fire as we reported (Jones et al. 2016). The decision to exclude the most severely burned territories represented an egregious analytical flaw and part of the reason Hanson et al. (2018) erroneously concluded that salvage logging, not high-severity fire, was responsible for the considerable decline in territory occupancy post-fire.

(2) Hanson et al. incorrectly claimed that Jones et al. (2016) underestimated or dismissed the potential influence of salvage logging. Hanson et al. (2018: 101) stated that Jones et al. (2016) "... dismissed post-fire logging as a factor in the reduced spotted owl occupancy that they reported one year after the fire." In fact, we (Jones et al. 2016) explicitly tested for the effect of post-fire salvage logging using a model-selection framework and determined it was statistically uninformative (Arnold 2010) at the 1100-m spatial scale. An additional analysis, performed by G. M. Jones (G. M. Jones, unpublished results), confirmed the same result at the 1500 m scale. Hanson et al. further state that, based on their own methods of quantifying salvage logging in the King Fire, they found more salvage logging than was reported by Jones et al. (2016), implying that Jones et al. under-reported salvage logging. However, the two studies shared only six territories (of the 21 salvage-affected territories in Jones et al.) rendering a direct comparison inappropriate. It is noteworthy that, of these six territories, three became extinct after the King Fire (ELD0058, PLA0039 and ELD0057), yet experienced only 0%, 0% and 0.2% salvage logging, respectively and all experienced between 60-70% high-severity fire. Thus, one must consider the profound difference in spatial extent of high-severity fire vs. salvage logging and its likely relative influence; within the 21 territories studied by Jones et al. (2016), where both high-severity fire and salvage logging occurred, high-severity fire was 17 and 12 times more prevalent on average than salvage logging at 1100-m and 1500-m scales, respectively.

(3) Hanson et al. used inaccurate data about the owl territory histories affected by the King Fire that were part of Jones et al. study area. The following errors likely stemmed from Hanson et al.'s lack of familiarity with our study area and using data they did not collect. The best example of data inaccuracy that led to inferential errors was Hanson et al. (2018) treating one territory (PLA0065) as unoccupied both before (2014) and after the fire (2015). However, this territory was unmistakably occupied by a banded pair of owls that fledged three young in 2014 and then became extinct after the King Fire (the burned remains of the territorial male were found near its nest site in 2015, see above). In a second example, Hanson et al. (2018) treated two spatially overlapping territories (PLA0039 and PLA0080) as being occupied both before (2014) and after (2015) the fire, even though these territories have not been simultaneously occupied by territorial owls during a single breeding season since 1996. However, because the two territories share a relatively large overlapping area (i.e. overlapping estimated territory areas based on average study area-wide nearest-neighbour distances), a single detection could occur within "both" territory areas (i.e. within the area of overlap). Thus, we assigned detections each year from PLA0039 and PLA0080 to a single territory where either nesting behaviour was observed during the breeding season or, if no nesting behaviour was observed, to the territory where the majority of detections occurred during that breeding season. Therefore, assigning the correct annual occupancy status to PLA0039 and PLA0080 required direct observational knowledge of both the study area and the behaviour of the birds in any given year - Hanson et al. (2018) lacked this critical information. As a result, Hanson et al. (2018) treated PLA0039 as occupied before and after the fire, but this territory actually became extinct after the fire. In this case, Hanson et al. assigned an owl detection to PLA0039 in 2015 that should have been assigned to an adjacent (and overlapping) territory (PLA0080) because PLA0080 represented the primary nest/roost area being utilised by colour-marked spotted owls in that year. By the same error, a detection that Hanson et al. assigned to PLA0080 in 2014 should have been assigned to PLA0039. Therefore, Hanson et al. assigned an incorrect pre- or post-fire occupancy status to 3 of 7 territories (43%) from the Eldorado study area and at least 3 of 10 (30%) King Fire-affected territories used in their analysis.

(4) Hanson et al. used partial datasets and inadequate analyses. Faulty inferences can easily occur when raw data are re-analysed without understanding the data collection process or the implications of one type of data versus another (e.g. the difference between a night-time location and a daytime location when assessing territory occupancy – see below). In contrast to Jones et al. (2016), Hanson et al. (2018) did not collect data on spotted owl occupancy themselves. Rather, they acquired data collected by the USFS and contractors. In the case of the King Fire, this information included summary data on spotted owl territory occupancy that we submitted to the USFS but did not include other information such as: (1) colour-band combination of owls at each territory; and (2) individual survey data. The USFS did not request the other information from us because they simply needed to know if any owls had been detected at a site, the pair status, presence of young and the exact location of the birds and nest (if present). As discussed above, without information on individual identity and time of detection during a survey, it was not possible for Hanson et al. to eliminate "false positive" detections resulting from owls using multiple territories during their nocturnal activities, which can lead to significant upwardly biased occupancy estimates (Sutherland

et al. 2013, Berigan et al. 2018). As they did not have survey-specific data, Hanson et al. (2018) were unable to use standard occupancy modelling approaches that account for imperfect detection (i.e. the possibility that an owl is present even if not detected), an issue well-known to lead to biased estimates of site occupancy (MacKenzie et al. 2006). Finally, in contrast to Jones et al. (2016), who used a natural Before-After Control-Impact experimental design that accounted for imperfect detectability, Hanson et al. (2018) analysed only post-fire naive occupancy patterns without considering imperfect detection of owls, which does not provide a robust test of fire effects.

(5) Hanson et al. are incorrect in their claim that Jones et al. (2016) overestimated territory extinction rates. Hanson et al. (2018) argued that we (Jones et al. 2016) overestimated the effect of high-severity fire on owls by inferring the extinction of eight owl territories (PLA0007, PLA0065, PLA0015, PLA0109, PLA0102, ELD0060, PLA0049 and PLA0043) that were actually unoccupied pre-fire (and therefore could not have become extinct). With the exception of one territory where Hanson et al. (2018) had incorrect data (PLA0065, where three owlets were fledged in the summer 2014 [see above]), Hanson et al. were *correct* that the other seven territories were unoccupied pre-fire but *incorrect* in that we (Jones et al. 2016) treated them otherwise. Indeed, we (Jones et al. 2016) treated these seven territories as unoccupied prefire. As the territories were unoccupied pre-fire, they made no numerical contribution to our (Jones et al. 2016) estimate of high extinction rates in high-severity- burned owl territories. In this last case, we have concluded that Hanson et al. (2018) apparently misunderstood the nature of local extinction, which is a first-order Markov process where an extinction event occurring at time t is conditional on that same unit being occupied at time t-1.

(6) Hanson et al. (2018) made incorrect or unsubstantiated claims about errors in the habitat selection analyses in Jones et al. (2016). We marked spotted owls with GPS backpacks and found that they avoided forests that burned at high-severity, but Hanson et al. claimed our inference was invalid for two reasons. First, Hanson et al. (2018: 101) stated that "... Jones et al. (2016) did not account for distance from site centres for this central place forager ... " - that is, owls were less likely to use areas further away from their central nest/roost area. While many other studies of spotted owl foraging have not explicitly accounted for this effect (e.g. Carey et al. 1990; Ganey and Balda 1994; Ganey et al. 2005; Hamer et al. 2007; Bowden 2008; Williams et al. 2011; Forsman et al. 2015; Comfort et al. 2016; also see Singleton et al. 2010 for barred owl), we (Jones et al. 2016: 303) did because we eliminated foraging locations beyond the 95th percentile of foraging distances so that "...distant areas rarely visited by owls in foraging bouts (Bond et al. 2009) were not counted as 'available' habitat. As a result, the analysis consisted of GPS locations that occurred within distance ranges used at relatively high frequencies...." Moreover, our result held even when we re-analysed the data using a continuous distance-to-centre covariate (Figure 1), which indicated that owls were over 2.5× less likely on average to use high-severity-burned forest than any other forest type (Odds Ratio(β_{severe}) = 0.38, 95% CI = 0.28, 0.54). A simple visual inspection of foraging locations for our GPS-marked owls demonstrated the strong



Figure 1. Mixed-effects logistic regression model showing foraging habitat selection (third order, use vs. available) by California spotted owls near or within the boundary of the 2014 King Fire. The model structure was $logit(y_i) = \beta_0 + \beta_1^*$ distance_i + β_2^* distance_i² + β_3^* severity_i + $\sigma_{individual}$ where the final term was a random effect for individual owls. The coefficient estimate for β_3 was -0.951 (95% CI = -1.28, -0.62) and the odds ratio was OR(β_3) = 0.38 (95% CI = 0.28, 0.54), indicating that owls avoided high-severity-burned forest relative to other severities and unburned forest.

avoidance of high-severity fire areas, particularly for owls whose activity centres were near the large, high-severity burned patch (Figure 2). Second, Hanson et al. claimed that spotted owls avoided high-severity-burned forest in Jones et al. (2016) because these areas included recent pre- and post-fire clear-cuts, suggesting spotted owls would have preferentially selected such areas had they not been logged. While spotted owls may indeed avoid such areas, data from Jones et al. (2016) unambiguously showed several clear examples of spotted owls avoiding large tracts of high-severity burn area that were *not* salvage logged (Figure 2). Without any specific analysis by Hanson et al., we conclude they were merely presenting assertions or unsubstantiated claims.

(7) Hanson et al. selectively referenced literature to support their conclusions. Hanson et al. (2018) either failed to cite, or cited but misinterpreted, research that supports negative effects of high-severity fire on spotted owls. First, Hanson et al. did not cite a recent paper by Rockweit et al. (2017) who also found a negative effect of high-severity fire on northern spotted owls (*S. o. caurina*) in north-western California.



Figure 2. Spotted owl movement patterns in and around the 2014 King Fire. Locations of spotted owl foraging activities that were collected in 2015 are represented by black dots. The King Fire extent (foot-print) is shown in grey and high-severity fire (> 75% canopy mortality) is shown in orange. The locations of known post-fire salvage logging operations on private lands that occurred prior to the end of data collection in 2015 are shown using black hatch marking (displayed in the inset examples). Large patches of high-severity-burned forest (orange) within spotted owl foraging ranges are clearly avoided. Data from Jones et al. (2016), but the graphical presentation here is different.

Although Rockweit et al. (2017) studied a different subspecies of owl, California and northern spotted owls have similar habitat associations and evolved in similar fireadapted forests. Second, Hanson et al. (2018) did not cite Ganey et al. (2017), who reviewed the spotted owl-wildfire literature and concluded that the loss of spotted owl nesting habitat to high-severity fire was sufficiently widespread to constitute a threat to the species' persistence. Third, although Hanson et al. cited two recent studies in which habitat use patterns of northern and California spotted owls were investigated in relation to fire (Comfort et al. 2016, Eyes et al. 2017), they failed to acknowledge that these studies supported the patterns reported in Jones et al. (2016). Here we have demonstrated that Hanson et al. (2018) used erroneous data, flawed statistical analyses, unsupported assertions and faulty inferences to reach their main conclusion that the King Fire did not negatively affect spotted owls and more generally that large, high-severity fires do not pose risks to spotted owls in dry forest ecosystems. While much remains to be learned about how and under what conditions high-severity wildfire affects spotted owl habitat and populations, research has provided a growing body of evidence that high-severity fire can have adverse effects on spotted owls. Territory occupancy declined immediately following the King Fire and GPS-tagged spotted owls avoided a large area of high-severity fire, independent of salvage logging (Jones et al. 2016); turnover rates were higher and survival lower for owls in territories affected by high-severity fires in north-western California (Rockweit et al. 2017); and owls avoided high-severity burned areas in both the Timbered Rock fire and fires in Yosemite National Park (Comfort et al. 2016, Eyes et al. 2017). Ignoring the potential for large, high-severity fire to affect spotted owls negatively could compromise the ability to conserve this species, particularly as climate change produces conditions that exacerbate the risk of high-severity fires (Abatzoglou and Williams 2016, Westerling 2016). As scientists we believe it is fundamentally more important to understand or acknowledge the negative effects of high-severity fires on spotted owls because failing to do so has the potential to impede forest restoration and efforts to reduce fire risk through management actions (Peery et al. 2019).

We do not recommend any particular management strategy because it is beyond our purview here, but we do suggest that forest ecosystem restoration activities that reduce the frequency and size of large, severe fires could benefit spotted owls if these activities are conducted properly (i.e. with consideration of spotted owl habitat and space use requirements), but we submit that the evidence is unambiguous that mega-fires can be a major threat to spotted owls and their habitat. Thus, we need to understand the nature of the threat(s) and how best to meet that threat through appropriate conservation strategies. We also do not profess to know the appropriate balance between retaining spotted owl habitat to promote viable populations in the short-term and implementing forest restoration activities to reduce large, severe fires in the long-term, but we must strive to find it or at least a range of conservation options. We believe that deriving such balance can best be achieved through an improved understanding of how wildfire affects spotted owls, how climate change affects future changes in wildfire regimes and forest conditions and by prospective modelling that links spotted owl dynamics to changing conditions. Forest ecosystem management, intended to reduce large, high-severity fires, is least likely to impact spotted owls in the short-term if they can be designed to retain forest structural characteristics known to be important to owls (Tempel et al. 2015, Jones et al. 2018). Clearly, meeting the dual objectives of spotted owl conservation and forest ecosystem restoration will be complex, but these objectives are not served by faulty science (Peery et al. 2019).

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Supplementary material I

Figure S1

Authors: Gavin M. Jones, R. J. Gutiérrez, H. Anu Kramer, Douglas J. Tempel, William J. Berigan, Sheila A. Whitmore, M. Zachariah Peery

Data type: Representative photographs of two spotted owl nest areas burned at high fire severity during the King Fire (2014) and three general areas within the Eldorado Study Area in the central Sierra Nevada, California, USA that depict three general fire severity classes of this fire.

- Explanation note: Nest site area within the spotted owl territory PLA0113 taken 7 months after being burned by the King Fire, central Sierra Nevada, California, USA. An estimated 90.7% of this owl territory (based on 1100 metre radius circle) burned at high-severity.
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Link: https://doi.org/10.3897/natureconservation.37.32741.suppl1

Supplementary material 2

Figure S2

Authors: Gavin M. Jones, R. J. Gutiérrez, H. Anu Kramer, Douglas J. Tempel, William J. Berigan, Sheila A. Whitmore, M. Zachariah Peery

Data type: Representative photographs of two spotted owl nest areas burned at high fire severity during the King Fire (2014) and three general areas within the Eldorado Study Area in the central Sierra Nevada, California, USA that depict three general fire severity classes of this fire.

- Explanation note: Nest site area within the spotted owl territory PLA0065 taken 7 months after being burned by the King Fire, central Sierra Nevada, California, USA. An estimated 95.5% of this owl territory (based on 1100 metre radius circle) burned at high-severity.
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Link: https://doi.org/10.3897/natureconservation.37.32741.suppl2

Supplementary material 3

Figure S3

Authors: Gavin M. Jones, R. J. Gutiérrez, H. Anu Kramer, Douglas J. Tempel, William J. Berigan, Sheila A. Whitmore, M. Zachariah Peery

Data type: Representative photographs of two spotted owl nest areas burned at high fire severity during the King Fire (2014) and three general areas within the Eldorado Study Area in the central Sierra Nevada, California, USA that depict three general fire severity classes of this fire.

- Explanation note: Example of a typical area within the contiguous >13,000 ha patch of high-severity fire that burned at high-severity on the Eldorado spotted owl study area located in the central Sierra Nevada, California, USA.
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Supplementary material 4

Figure S4

Authors: Gavin M. Jones, R. J. Gutiérrez, H. Anu Kramer, Douglas J. Tempel, William J. Berigan, Sheila A. Whitmore, M. Zachariah Peery

Data type: Representative photographs of two spotted owl nest areas burned at high fire severity during the King Fire (2014) and three general areas within the Eldorado Study Area in the central Sierra Nevada, California, USA that depict three general fire severity classes of this fire.

- Explanation note: Example of a typical area within the contiguous >13,000 ha patch of high-severity fire that burned at high-severity on the Eldorado spotted owl study area located in the central Sierra Nevada, California, USA.
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Supplementary material 5

Figure S5

Authors: Gavin M. Jones, R. J. Gutiérrez, H. Anu Kramer, Douglas J. Tempel, William J. Berigan, Sheila A. Whitmore, M. Zachariah Peery

Data type: Representative photographs of two spotted owl nest areas burned at high fire severity during the King Fire (2014) and three general areas within the Eldorado Study Area in the central Sierra Nevada, California, USA that depict three general fire severity classes of this fire.

- Explanation note: Example of an area burned at moderate-severity within a spotted owl nest stand used in 2015 (ELD0085) on the Eldorado spotted owl study area located in the central Sierra Nevada, California, USA. In this case, the original territory centre (i.e. 2014) was ~1 km from this new nest stand but was burned at high severity. In addition, this female paired with the male displaced from PLA0113 (see Figure S1) by high-severity fire.
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Supplementary material 6

Figure S6

Authors: Gavin M. Jones, R. J. Gutiérrez, H. Anu Kramer, Douglas J. Tempel, William J. Berigan, Sheila A. Whitmore, M. Zachariah Peery

Data type: Representative photographs of two spotted owl nest areas burned at high fire severity during the King Fire (2014) and three general areas within the Eldorado Study Area in the central Sierra Nevada, California, USA that depict three general fire severity classes of this fire.

- Explanation note: Example of an area burned at low-severity on the Eldorado spotted owl study area located in the central Sierra Nevada, California, USA. This area had natural open areas of brush and rock with continuous patches of forest that incurred low tree mortality. This area contained no spotted owl territory.
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RESEARCH ARTICLE



The Un-Common Leopard: presence, distribution and abundance in Gallies and Murree Forest Division, Northern Pakistan

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Abstract

The leopard Panthera pardus is thought to be sparsely distributed across Pakistan and there is limited understanding of the demographic structure and distribution of the species in this country. We conducted a study, from April to July 2017, and, from March to June 2018, in the northern Pakistan region to establish the presence and distribution of leopards, mindful at the outset of their abundance in that region. The presence of leopards was confirmed in the Swat, Dir and Margalla Hills region. The leopard population in Gallies and Murree Forest Division was preliminarily assessed via camera-trapping. As a result, a total of 63 potential areas of leopard population were identified initially. The leopard was photo captured at 27 locations (hotspots) with 34 capture events yielding 195 images over the course of 3,022 active trap-nights. Camera trap images were examined to identify leopard individuals using their rosette patterns on both the left and right flanks and the dorsal side of the tail. Ultimately, 15 leopard individuals were identified during the first survey period of the study and four individuals were recaptured in the second survey period, together with three new individuals. The detection probability of individual leopards from MARK varied from 0.10 and 0.20 with a population size (preliminarily estimated to be 16-25 (SE = 3.18) in 2107 and 7-13 (SE = 1.87) in 2018. This gave a density of 4.5 to 9.5 leopards/100 km², respectively. A home range of various individual leopards was found to extend from the Gallies Reserved Forest to the extended corridors of Guzara Forest. In general, this study suggests that the Guzara Forest is crucially important for the conservation of leopards in the region as this area allows them extended movement while searching for food and mates.

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Keywords

Leopard, Panthera pardus, individual recognition, camera trapping, presence/absence, Northern Pakistan

Introduction

The leopard is one of the most widespread territorial mammalian carnivores on earth (Nowell and Jackson 1996; Hunter et al. 2013; Ripple et al. 2014). The solitary and opportunistic nature of this species enables it to be highly adaptable to different environmental conditions, which range from Africa to the Middle East, Asia, through to the far north of Russia, and then eastwards to Southeast Asia (Nowell and Jackson 1996; Dickman and Marker 2005; Stein and Hayssen 2013). Leopards are found in a wide range of habitat types from tropical, subtropical and humid forests, mountain, savannah and scrub through to deserts (Nowell and Jackson 1996; Sanei et al. 2011a; Stein and Hayssen 2013; Shehzad et al. 2014; Athreya et al. 2016). They feed on a broad range of prey species, such as ungulates, birds, rodents and reptiles (Sanei et al. 2011b; Mondal et al. 2012a; Shehzad et al. 2014; Kshettry et al. 2018). Leopards are wide-ranging carnivores. They defend their territories and maintain their home ranges for natural ranging and foraging activities. Brown and Orians (1970) define territories as 'a fixed, exclusive area with the presence of a defence that keeps out rivals'. The concept of a home range is described as an area in which the animal pursues food or engages in routine activity (Jewell 1966; Burt 1943). Leopards also persist in high 'human-use' areas (Athreya et al. 2016; Kshettry et al. 2017). However, despite all these flexible characteristics, the leopard population is declining throughout their species range. As a result, leopards are now absent from 63–75% of their historical range, with the highest rate of decline in Asia where several subspecies are characterised as endangered (Stein and Hayssen 2013). Jacobson et al. (2016) demonstrated that leopards have disappeared from 83-87% of their former range in Asia, while the distribution in Africa has declined to around 48–67% of their former distribution (Sheikh and Molur 2004; Ghalib et al. 2007; Laguardia et al. 2015; Sanei et al. 2016).

The main threats to leopards include habitat loss and degradation, developments close to protected areas, rapid depletion of the natural prey base, poaching, and conflicts with livestock causing revenge killing by the livestock owners (Fahrig 2003; Athreya and Belsare 2007; Mondol et al. 2009; Sanei and Zakaria 2011c; Sanei et al. 2012; Kabir et al. 2013; Qi et al. 2015). Isolation and fragmentation of habitats are further threatening the leopards within their remaining ranges by undermining the genetic health of the populations (Spong et al. 2000; O'Brien and Johnson 2005; Quaglietta et al. 2013).

In this study, we aim to establish baseline information for long-term monitoring of leopards to further improve the management and conservation of the species in the Gallies and Murree Forest Division in northern Pakistan. The findings will also provide a general understanding about leopard habitats in Pakistan. The objective of this current study is to establish baseline information for the long-term monitoring and effective management of leopard conservation in the Gallies and Murree Forest Division. The approach will provide a model for other leopard habitats in Pakistan. This approach also provides additional information on the presence of prey species for leopards in the area.

Leopards in Pakistan

In Pakistan, leopards were once widely distributed across the country in a variety of habitats and regions such as Punjab Baluchistan, Khyber Pakhtunkhwa, Sindh, Azad Jammu and Kashmir (Roberts 1977). Leopards are now known to be sparsely distributed across the country (Sheikh and Molur 2004; Henschel et al. 2008; WWF-Pakistan 2014). A principal reason for this is deforestation (only about 2.5% of the original forests remain) with an annual rate of decline of forest cover of 2.1% (FAO 2007). The erosion of land as well as landslides, mainly due to high deforestation, private land ownership in the surrounding Guzara Forest of protected areas, and the right of local communities to collect fuel wood within these zones, are further threatening these habitats (Ashraf et al. 2014).

In Pakistan, the leopard is classified as critically endangered in the Conservation Assessment and Management Plan developed by the IUCN (Sheikh and Molur 2004; Henschel et al. 2008). As habitats in Pakistan are increasingly populated by humans, there has been a decline in the local leopard populations and ranges, as well as their prey species, and livestock-leopard conflicts have increased (Uphyrkina and O'Brien 2003; O'Brien and Johnson 2005; Mondol et al. 2009; Ripple et al. 2014). Leopard attacks on humans occur occasionally across northern Pakistan (Lodhi 2007) and several leopards are poisoned or shot annually in reprisals (Muhammad Asad, pers. obs as Conservation Officer (2013–2014). Six leopard mortalities were reported in Ayubia National Park and the surrounding Guzara Forest between November 2011 and December 2012 after two children were attacked and killed (Khyber-Pakhtunkhwa Wild-life Department and WWF-Pakistan). It is likely that many leopard mortalities are not reported (Personal communication). For example, we found two leopard bodies with their skin removed in the Gallies Forest Division during our data collection for this study that had not been reported to Khyber-Pakhtunkhwa Wildlife Department.

Other threats to leopards include poaching, trapping cubs for animal dealers, and the trade of body parts and skins. Skin, claws, and teeth are available for sale in markets in northern Pakistan (Personal communication. Theile 2003; Ripple et al. 2014). Leopards are protected under the law but rules and regulations are poorly implemented on the ground, as there are no checks and balances within the limited management capacity of local wildlife departments.

The lack of a compensation programme to recompense livestock owners for relative losses, e.g. in Swat and Dir regions, or slow compensation procedures, e.g. in Gallies Forest, further undermine leopard conservation by causing local people to resent leopards (Shehzad et al. 2014).

Leopard vulnerability to extinction is higher than for other cats due to their wideranging natural movements for food and mates as this exposes them to higher risks (Cardillo et al. 2004). Stein et al. (2016) suggested a sparse distribution of leopards in Waziristan, Sindh, Punjab, and Ayubia National Park. However, knowledge of species abundance and density is vital for conservation efforts at both the species and population levels (Williams et al. 2002; Royle and Dorazio 2008). Knowledge about the status of leopard distribution and density is vital for successful conservation and management programmes (Borah et al. 2013; Jacobson et al. 2016). This allows for the allocation of appropriate resources, the development of effective mitigation measures, adaptive responses by wildlife managers in case of conflict, and the prioritisation of conservation efforts in high-value habitats.

In Pakistan, there are no robust estimates for the current distribution and density of leopards. Phylogenetic analysis confirms the presence of two subspecies P. p. saxicolor, P. p. fusca (Asad et al. 2019). Few studies on diet analysis and conservation have been conducted that address human-leopard conflicts (Lodhi 2007; Kabir et al. 2013; Shehzad et al. 2014), although these studies at least indicate the presence of leopards in different areas (e.g. Galyat, Azad Kashmir and Sindh). Khan et al. (2013) assessed the current distribution and status of mammals, including leopards, in the Khirthar protected area. Anecdotally, the leopard is assumed to have a stable population in northern Pakistan, including the Swat, Dir, and Margala Hills regions (Shehzad et al. 2014). However, the local people and the Wildlife Department in Khyber Pakhtunkhwa (Province) believe that the species has disappeared from the Swat and Dir districts. Recently, the presence of leopards has been confirmed in the Ayubia National Park and the surrounding Forest Reserve of Khyber Pakhtunkhwa and Murree following the detection of leopard scats (Shehzad et al. 2014). Observations of human-leopard conflicts have been made in the Machiara National Park, Azad Jammu and Kashmir, and the Ayubia National Park by Lodhi (2007) and Kabir et al. (2013).

Estimating the presence of leopard populations is difficult as they have large ranges in their natural habitats and usually occur at low densities (Tobler and Powell 2013). Observations of human-leopard conflicts have been made in Machiara National Park, Azad Jammu and Kashmir, and Ayubia National Park, by Lodhi (2007), Kabir et al. (2013) and Shehzad et al. (2014), who analysed the diet of leopards in Ayubia National Park. Many of these also act as conservation studies and so are important for understanding the ecology and behaviour of the top predators in specific ecosystems and for the effective conservation of the species (Brodie 2009). Meetings and semistructured interviews have been used to ascertain leopard presence-absence from regions (Abdollahi 2015). Semi-structured questionnaires were used to collect presenceabsence information from villagers in Swat (Ahmad et al. 2014) and their presence was confirmed by installing camera-traps to collect spatial and temporal information and develop a picture of species distribution (Mondal et al. 2012b). The presence-absence data of a species is vital for researchers in conservation-related efforts, particularly for cryptic carnivores (MacKenzie 2005). Therefore, sampling with multiple procedures and combining sampling processes is often required to construct reliable presenceabsence datasets (Manly et al. 2002; MacKenzie 2005).

Obtaining information about abundance, predictability, and site occupancy is challenging over the range of habitats that leopards inhabit, as they have a wide range and occur in low densities (Balme et al. 2009; Kery et al. 2010). Closed populations and capture-recapture frameworks have been used to estimate the abundance of many elusive carnivores, such as tigers (*Panthera tigris*) and leopards (Karanth 1995; Wang and Macdonald 2009; Wegge et al. 2009), jaguars (Sollmann et al. 2013; Tobler and Powell 2013), ocelots (Trolle and Kery 2003), clouded leopards (Borah et al. 2013), and snow leopards (Alexander et al. 2016). These frameworks require all individuals to be identifiable and to have reasonably high capture probabilities, with a random sampling of individuals (Harmsen et al. 2011).

Estimates of felid presence include abundance and density estimates for the common leopard and the clouded leopard in Manas National Park (Borah et al. 2013), estimates of a tiger population from camera-trap data (Karanth 1995; Wang and Macdonald 2009), estimates of jaguar density with camera-traps (Tobler and Powell 2013), and estimates of grazing mammal densities using camera-traps (Rowcliffe et al. 2008).

Camera-trapping has recently emerged as a promising method for estimating the abundance of elusive carnivore species in ecological sciences by identifying individuals through their unique pelage patterns with minimal disturbance (Karanth 1995; Heilbrun et al. 2003; Henschel and Ray 2003; Alonso et al. 2015). Camera-traps are a useful technique for observing and assessing animal information in situ (Khorozyan et al. 2008; Balme et al. 2009; Tobler and Powell 2013; Bashir et al. 2014). As such, camera-traps have been adopted widely for detecting the presence, abundance, and the proportion of sites occupied by a species (Kery et al. 2010). Camera-traps and fieldbased surveys obtain sufficient spatial and temporal information for the species that are present within the sample unit to estimate the total population for an entire area (Henschel and Ray 2003; Silver et al. 2004; Jackson et al. 2006; Rowcliffe et al. 2008; Maffei and Noss 2008; Wang and Macdonald 2009; Sundaresan et al. 2011; Sollmann et al. 2013; Karki et al. 2013; Bino et al. 2014). As a territorial animal, a leopard generally does not leave a territory unless removed by humans or killed. Males usually show less variation in movement patterns than females, although the distance travelled by both sexes is similar, except around birth (Morten and Per 2005). We assumed that any differences in movement patterns between the sexes would not affect our closed population assumption because we sampled over the same season. Encounter histories were constructed from individual leopards observed in each sampling period (Silver et al. 2004; Wang and Macdonald 2009; Alonso et al. 2015).

Capture-recapture methods have been widely used to estimate abundance and density from camera photos in many carnivores, such as the snow leopard (*Panthera uncia*), tiger (*Panthera tigris*) (Sharma et al. 2010), bobcat (*Lynx rufus*), (Alonso et al. 2015), black bear (*Ursus americanus*) (Fusaro et al. 2017), jaguar (*Panthera onca*), (Silver et al. 2004) and common leopard (*Panthera pardus*) (Harihar et al. 2009). MARK capturerecapture (CMR) has also helped quantify distribution and abundance of prey (Otis et al. 1978; Karanth 1995; Soisalo and Cavalcanti 2006; Jackson et al. 2006; Balme et al. 2009; Alonso et al. 2015). The CMR framework presents an advantage if individual animals are able to be identified from their unique pelage patterns as this allows individual encounter histories to be constructed on different occasions using this framework (Soisalo and Cavalcanti 2006; Alonso et al. 2015). Population size and capture probabilities of the target species may be estimated (Alonso et al. 2015) and produce robust population estimates for many elusive carnivores (Heilbrun et al. 2003; Jackson et al. 2006; Balme et al. 2009; Rozhnov et al. 2015; Thornton and Pekins 2015).

The same robust approach was used in this study to estimate the abundance of common leopards in the Gallies and Murree Forest Division of Pakistan. A CMR model combined with Arc GIS mapping was used. CMR analysis is used to estimate abundance for closed and open populations (Karanth 1995; Borah et al. 2013; Alonso et al. 2015). A closed population allows a more robust estimate of population size than an open model, assuming there are no births, deaths or migration during the study period (Otis et al. 1978; White and Burnham 1999; Jackson et al. 2006; Balme et al. 2009). Several studies have used the average of mean maximum distance moved MMDM or 1/2 MMDM for individuals captured by more than one camera-trap. A buffer is then estimated around each camera-trap to calculate the estimated sample area (ESA) (Karanth and Nichols 1998; Sollmann et al. 2013; Tobler and Powell 2013). The ESA is considered more accurate if calculated with the buffer of a full MMDM, which is believed to be larger for species with large home ranges (Silver et al. 2004; Soisalo and Cavalcanti 2006; Sollmann et al. 2013). A small sample area could mislead and allow overestimation of a population size (Harmsen et al. 2011; Tobler and Powell 2013; Thornton and Pekins 2015). We estimated the number of leopards that we didn't see and added to those that we did (abundance) from CMR and then calculated how many there are in an area (density).

Materials and methods

Study area

The study was conducted in northern Pakistan, across the Gallies Forest Division $(34^{\circ}04'07''N, 73^{\circ}41'03''E)$, Murree Forest Division $(33^{\circ}52'26.34''N, 73^{\circ}23'42.21''E)$, Swat $(35^{\circ}01'10.70''N, 72^{\circ}08'50.93''E)$, and Dir districts $(35^{\circ}51'11.19''N, 72^{\circ}50'30.46''E)$ and the Margalla Hills region $(33^{\circ}44'23.99''N, 73^{\circ}2'18.00''E)$.

The area of the Gallies Forest Division comprises a 15,716 ha Reserve Forest and a 8,224 ha Guzara Forest, which is also managed by the Khyber Pakhtunkhwa Forest Department. The Ayubia National Park is located in the Forest Reserve of Gallies Forest Division with a total area of 3,312 ha surrounded by other Reserved Forest. The Guzara Forest of the Gallies Forest Division is linked to the Reserved Forest that is surrounded by five villages. The boundaries of the Reserve Forest and Guzara Forest are disputed (Lodhi 2007). Guzara Forest acts as a corridor that allows species to extend their movement into an area with low human densities while searching for food (Fig. 1). The main source of income for local people is seasonal tourism and livestock (Lodhi 2007). The total area of the Murree Forest. The Murree Forest Division manages 22 Protected and 23 Reserve Forest patches (Ashraf et al. 2014; Ahmed and Mahmood 1998). Most of the available knowledge on Pakistani leopard presence-absence, diet and human leopard conflicts are only available for these places, so it is assumed that they have rela-

tively stable leopard populations (Shehzad et al. 2014). The total area of the Margalla Hills is 17,386 ha. The Margalla Hills is an extension of the Islamabad Wildlife sanctuary that includes Shakar Parian Hills and Rawal Lake (WWF-Pakistan).

Our study area lies in the outer Himalayas in the sub-tropical continental highlands and encompasses two distinct ecological zones, 'moist temperate coniferous forests' and 'chir pine subtropical forests' (Ashraf et al. 2014). Mammals within the sampled area include the leopard cat, *Prionailurus bengalensis*, jackal, *Canis aureus indicus*, rhesus monkey, *Macaca mulatta*, marten, *Martes flavigula*, Indian palm civet, *Paradoxurus hermaphroditus*, Himalaya palm civet *Paguma larvata* and red fox, *Vulpes vulpes* (Shehzad et al. 2014). There are no recent forest maps in Pakistan that include Guzara Forest, except for the Murree Forest Division, and the Ayubia National Park that were developed by WWF-Pakistan during delineation of the forest boundaries (Ashraf et al. 2014; Abbas et al. 2010). We delineated the boundary between Reserved Forest and Guzara Forest with the help of ArcGIS from the old maps provided by the Khyber-Pakhtunkhwa Wildlife Department (Fig. 1).

Questionnaire survey

Between April 2017 and March 2018, we conducted questionnaire surveys (n = 1028) among local communities living close to the study areas of Galyat, Murree, Margalla Hills, Swat and Dir where they were asked to identify potential sites for detecting leopard presence. Around 30 questionnaires were completed at each village; in total, there were 35 villages. These villages were randomly selected from the union council map and, within each village, interviewees were randomly selected. The following information was collected: livestock depredation, time of attack, and type of injury, e.g. bite marks on neck or missing dogs or human casualties. Where possible, we validated the collected data by visiting each site as well as interviewing local Khyber Pakhtunkhwa Wildlife Department staff and nomads.

A total of 69 leopard records were identified from the questionnaire surveys. Out of these, 39 records were from Galyat and Murree, 24 from Swat and Dir, and 6 from Margalla Hills National Park. Six locations were later discarded from Galyat region due to the doubling of locations with different names, giving a final count of 63 sampling sites. Data were used to choose sites for future tracking surveys and camera-trapping (Fig. 1).

Tracking survey

We conducted surveys in selected sites where leopards had been reported. Each trail surveyed was 4–10 km in length and was completed between 0700 and 1700 hr. We searched trails for signs of scats, territorial markings, and tree scratches that implied leopard presence-absence. Signs of leopards were recorded and photographed. Areas were identified on the trails that had frequent leopard movements (Fig. 2). Such loca-



Figure 1. Sampling locations of the camera-traps survey in Gallies Forest (Ayubuia National Park, surrounding Reserved Forest and Guzara Forest), and Murree Forest (Protected, Reserved and Municipal Forest) **A** Country map (top left – green) followed by **B** study area showing different city boundaries **C** showing legend

tions were used as sites for the camera-traps. We were not able to sample from the Margalla Hills Region due to the insufficient number of camera-traps available and relied on transect sampling data for confirmation of leopard presence-absence.

Secondary data on leopard attacks on humans that resulted in injuries or deaths, cases of revenge killing, as well as leopard natural deaths when detected, were collected from Khyber Pakhtunkhwa Wildlife Department and WWF –Pakistan for the years 2005–2018 for the district of Abbottabad.

Camera trapping

We conducted camera-trap surveys along the tracking trails in 63 locations across Galyat and Muree, Swat and Dir. Camera-trapping was conducted, from April to July 2017 and from March to June 2018. The survey was carried out in summer because of heavy snowfalls in winter. The study area was divided into three sections: Galyat and Murree, Swat and Dir, and the Margalla Hills. We deployed 14 camera-traps in two sections (a total of 63 locations) for a period of 14 days at 20–40 cm above the ground (Balme et al. 2009).

Leopards are generally nocturnal and most active during dawn and dusk (Ray-Brambach et al. 2018). Thus to extend the battery life, the camera-traps were only active between 6 pm – 8 am. Nomadic farmers and their grazing livestock were generally active during the daytime. Also, male and female leopards have different activity patterns over a 24-hour period. (Ray-Brambach et al. 2018). The camera-traps were



Figure 2. Representation of the study area with the effective sample area of the different hotspots identified. The buffer shows the MMDM from the leopards captured more than once from different locations. The hotspots were linked with the number of signs found on each track. The trails were named by the closest village, and the leopards were named according to the track on which they were photographed.

checked every two weeks to replace the batteries and re-position the cameras, if required. Camera angles, trigger speed, detection zones and time-lapse between the triggers were set according to the previous literature about installation considerations (see Rovero et al. 2013; Trolliet et al. 2014 and details below).

Two cameras, one on either side of the trail, were placed at each site facing each other, to capture both flanks of a passing leopard.

This allowed the identification of individual leopards from their unique rosette of spots (Karanth 1995; Heilbrun et al. 2003; Silver et al. 2004). Cameras were set with a high trigger speed (0.2–0.8 seconds) with a recovery time of 1 and 0.5 seconds, respectively, for the two cameras. Three photos per trigger were taken to capture leopards as they move faster on trails than in other topography types (Scheibe et al. 2008). The photographs were then manually examined for leopard detections. We relied on transect sampling data in the Margalla Hills as we did not have a sufficient number of camera-traps or time to complete the standard method.

A preliminary abundance estimate

To estimate the abundance in Galyat and Murree, where the leopard population is considered stable (Shehzad et al. 2014), camera-trapping was repeated for a second season, from March-June 2018. Camera-traps were also placed in the five connecting trails identified earlier through the preliminary survey in the locations where no leopard signs were found. This was to satisfy the assumption that no animals have zero capture probability (Balme et al. 2009) as leopards may use areas but leave no sign. Neither are they detected by locals.

The spacing of camera-traps was based on the minimum home range recorded for an adult female leopard with cubs, 5.2–6.6 km² in Nepal (Morten and Per 2005) and 8 km² in north-central Namibia (Dickman and Marker 2005). Most studies show that the home range size varies in female leopards around birthing time (Rozhnov et al. 2015) while the distribution of prey and the location of females most affects the home range size in males (Bailey 1993; Odden and Wegge 2005). Since the width of trails varies from 0.5–3 metres, it was not practical to obtain detailed images of both flanks on trails with less than 1 m width. On wider trails (i.e. over 1 m width), the cameras were set at a 90° angle from the direction of the trail to obtain images of both flanks of every passing leopard. It was difficult to obtain detailed images of both flanks on trails less than 1 m in width. Cameras were set at a 45° angle on trails with less than 1 m width for obtaining clear images required for the subsequent individual identifications.

The sex of individuals was identified by their distinctive morphological features (Balme et al. 2012), and each identified individual was given a name based on the track that they were recorded in. Camera-traps were moved frequently from one location to another after 14 days, as we discovered new trails with leopard sign. Individual leopards were identified from their unique rosette patterns, based on the guidelines from Heilbrun et al. (2003) and Jackson et al. (2006). The independence of events was addressed on the basis of instructions provided in the same references. We used the

image manipulation programme GIMP, available online at http://gimp.org to digitise unique noticeable spots found in different areas of the body. We analysed spot to spot to differentiate individuals from one another.

Preliminary mark-recapture practice

The MARK Program (Version 8.2; White and Burnham 1999) was used to estimate the abundance of leopards (White and Burnham 1999; Alonso et al. 2015). As a requirement of the model, the population is assumed to be closed with no natural mortality and permanent movements into or out of the survey area over this period. We believe that we met this assumption because of the short duration of the study.

The capture histories were constructed for 14-day sampling periods for each leopard simply by defining each day and night as a single session, resulting in 14 sampling occasions, to provide the maximum number of capture histories. We fitted seven priori models (plausible simple models with different combinations of covariates) to the data, which represent different combinations of factors that may affect capture probabilities: behaviour (probability of recapture of a different individual comparing to the probability of the first capture), individual heterogeneity, year, and survey night. The models are notated with the factors affecting capture probability indicated in parentheses. The data from each year were entered as different groups in the software to enable parameters to be shared between the two years. Models were compared using AIC, and model averaging was used to obtain overall abundance estimates. To estimate density from the abundance data, we determined the effective study area by calculating the buffer (the average of the maximum distance travelled between capture locations Fig. 3) around each camera-trap, as determined by MMDM. (Sollmann et al. 2013; Tobler and Powell 2013; Karanth and Nichols 1998). The density of leopards was calculated from the abundance data generated by Program MARK D = N/A, where A is the area covered during the sampling period (effective study area) and N is the number of leopards estimated by Program MARK.

Results

Presence and absence

In Galyat and Murree we recorded 192 leopard photos over 1,930 trap-nights, representing a capture success of 9.94 captures/100 trap-nights. We also located 58 territorial markings that included scats, scrapes and tree scratches. Most camera-trap photos (67%) were caused by the movement of local people and mostly from four camera stations Lalazar track, Pipeline track, Baragali track and Nagribala track. Non-target species, such as the fox, jackal, porcupine, wild boar, martens, rhesus monkey, and civet, comprised 21% of the images. Domestic livestock (goats and cows) represented 8.7% of the total images; false triggers, where there was no obvious reason for activation, comprised a relatively low 2% (Table 1).



Figure 3. Box plot showing distance travelled by identifiable male and female leopards captured at multiple locations in our study area.

In Swat and Dir we recorded one leopard at one camera-trap station from Shangla (Swat) over the 1,092 traps nights and located only two territorial markings in Nehagdara (Upper Dir) while scoping trails for leopard signs. We collected a total of 11,806 photographs, which mainly comprised the movements of livestock (sheep, goats, and horses) of the nomads (34%), local community, including hunters, contributed 32% of the total images. Nomads are people who travel from the plains to the hills during the summer to graze their herds (sheep, goat, cattle) and local communities are the people resident in the area for all of the year. False triggers and non-target species (e.g. foxes, jackals, porcupines, dogs, and domestic cats represented 18% and 14% of the total images respectively (Table 2)).

In the Margalla Hills, we conducted a walking survey for leopard signs at six locations across the area along 4–10 km-long transects, between 0700 and 1700 hr. We found four signs of leopard territorial marking as well as scats on four survey sites, which confirmed the presence of leopards in the area.

Individual recognition

We examined each individual leopard image for their unique spot pattern. The most distinctive body parts used for identification and comparison were the left and right flanks and the dorsal surface of the tail (Figs 4–6). A total of 15 individuals were identified during the first survey and four of them were recaptured in the second survey along with three new individuals. Leopards were recorded from 27 out of 39 hotspots (potential area of high leopard use) identified in the questionnaires or by previous

Table 1. Summary of the camera-trap images from 39 hotspots/trails for common leopard and non-target species showing active trap-nights, total photos and false images in Gallies and Murree Forest Division 2017 and 2018.

Sampling	Hotspots/	Active trap-	Total photos	False images	Non target capture			Common leopard			
period	trails				Other	Livestock	Local community	Photos	Captures	Initial capture	Un- identified
		nights			species				events		
2017	39	950	21,410	281	3,480	1,186	16,342	121	33	15	7
2018	39	980	8,221	328	2,927	1,455	4,040	71	21	Recaptured- initial capture	4
										4 3	

Table 2. Summary of the camera-trap images and trail scoping for presence-absence of the common leopard and non-target species at different location sampling periods and sites, showing active trap-nights, total photos and false images in 2017 and 2018.

Location	Sampling period	No of Active		Total	False]	Non target c	Common leopard		
		sites	trap-nights	photos	images	Other species	Livestock	Local community	Photos event	Territorial markings
Galyat and Murree	April – July 2017 March – July 2018	39	1,930	30,231	609	6,407	2641	20,382	192	58
Swat and Dir	March – June 2018	24	1,092	11,806	2,140	1,677	4,116	3,870	3	2
Margalla Hills	March – June 2018	6	-	-	-	-	-	-		4

signs). A total of 18 individuals were identified based on their unique rosette patterns. Leopard ID 01, an adult male, was observed on three separate trails that were adjacent. Four males and three females were observed on two trails with overlapping home range, and the rest of the identified leopards were observed on individual trails. Leopards from eight hotspots were not identified during the second year, as there were no clear images showing their distinguishing spots.

Preliminary abundance estimate

A summary of the model selection process is given in Table 3, where models are ranked according to AICc (Akaike information criterion is a technique that uses in-sample fit to estimate the likelihood of a model to predict/estimate future values (Akaike 1974). The top-ranked model assumes a constant capture probability, while the second-ranked model allows different capture probabilities in each year. The small difference in -2*log-likelihood suggests that the additional parameter explains little additional variation in the models. All models produced similar estimates for the leopard abundance for each year. Models that allowed for capture heterogeneity, p(het),pi(.), p(Year+het),pi(.), were not ranked highly by AICc which suggests some evidence of heterogeneity. The model-averaged abundance estimates for Galyat and Murree include 19, in 2017, and 9, in 2018, with 95% confidence intervals for 16–25 (2017) and 7–13 (2018), respectively, in the effective sample area of 200 km² derived from MMDM.

ANALYZED SPOT TO SPOT



Figure 4. Example of Individual identification of the same male leopard based on its unique rosette pattern on the dorsal surface of the tail captured in two different locations at Gallies Forest Division Khyber Pakhtunkhwa Pakistan (Muhammad Asad-Lincoln University).

Table 3. Model selection results from MARK analysis for common leopard population in Gallies Fe	orest
Division and Murree Forest Division Pakistan 2017–2018.	

Without behaviour models		AICc	Num.	-2*log-	20	2017		2018	
Model	Delta AICc	Weights	Par	likelihood	Estimate	SE	Estimate	SE	
p(.)	0.00	0.62	1	139.19	18.97	2.82	8.86	1.73	
p(Year)	1.96	0.23	2	139.09	19.36	3.30	8.53	1.80	
p(het),pi(.)	4.13	0.08	3	139.19	18.97	2.82	8.85	1.73	
p(het),pi(Year)	5.70	0.04	4	138.65	19.91	3.59	8.88	1.82	
p(Year+het),pi(.)	6.15	0.03	4	139.09	19.36	3.30	8.53	1.80	
p(Year*t)	20.35	0.00	14	130.54	19.08	3.15	8.35	1.67	
					19.10	2.99	8.77	1.76	
				lowe	er 16.77		7.61		
				upp	er 24.54		12.16		

The mean distances travelled by four adult male and three adult female leopards were 7 km and 4.6 km, respectively. We used a 6 km buffer (Fig. 2), for each camera trap, derived from the mean maximum distance moved by four adult males and three



Figure 5. Example of individual differences of the leopards based on the prominent dorsal surface of a tail captured in different trails at Gallies and Murree Forest Division (Muhammad Asad-Lincoln University).



Figure 6. Example of individual differences based on the prominent left flanks of three different individuals (**a**, **b**, **c**) captured on different trails in Gallies and Murree Forest Division.

adult females with more than one capture event on more than one camera trap (Fig. 3). Accordingly, the estimated leopard density at 200 km² was concluded as 9.5 individuals/100 km² in 2017 and 4.5 individuals/100 km² in 2018. The total estimated area of the Gallies and Murree forest Division is approximately 430 km², giving a total

population estimate, if leopards are potentially found in all habitats in this region, of 40 leopards in 2017 and 19 in 2018.

Individual sexes were identified from their external morphological characters. Eleven males and seven female leopards were identified. The sex ratio of male to female leopards in the study area, according to the camera-trapping, was 1.5:1.0. The mean encounter rate of females was higher than males on individual trails. The number of identified hotspots and leopard encounters was highest in Guzara Forest. The lowest numbers of hotspots and encounters were identified in the Cantonment and Municipal Forest (see Fig. 7).

Based on records obtained from the Wildlife Department Khyber Pakhtunkhwa and WWF-Pakistan in Abbottabad District, the mean number of leopards killed per year was 2.8 \pm 0.50. Eight leopards also died in captivity, including two cubs. Two leopard bodies were found during our camera-trap survey, in 2018, that were not reported but that showed signs of illegal hunting (their skins were removed). The overall number of leopards that died in the winter was the same as that in the summer although more males were killed in the summer than the winter, whereas more females were killed in the winter than the summer (Fig. 9). 21 attacks on humans were registered between 2005 and 2018 and, in response, 40 leopards were killed in retaliation (Fig. 8). The mean number of leopard attacks per year was 1.5 \pm 0.60. Ten of the attacks were lethal and the other 11 caused severe injuries.



Figure 7. Number of hotspots identified in different land uses in the Galyat and Murree Forest, independently captured through camera-traps and individuals identified on each trail; Protected Forest, Reserved Forest, Municipal Forest, Ayubia National Park, Guzara Forest, and Cantonment area.



Figure 8. Number of leopard attacks on humans (red triangles lethal, green squares injuries) vs. number of leopards killed in the district of Abbottabad from 2005–2018.



Figure 9. Number of male and female leopards that died in two seasons in the district of Abbottabad.

Discussion

Our study confirmed the existence of leopards in the Swat, Dir and Margalla Hills regions of Pakistan. Combined with a MARK-recapture model, our camera data provided a first estimate for the leopard population in the Gallies and Murree Forest Division. The preliminary questionnaire survey was useful in identifying the information related to hotspot/trail and allowed us to cover a large area of rugged terrain, with limited accessibility, to maximise the detection probability and monitor population abundance.

The data for abundance was collected over two sampling periods, April – July 2017 and March – June 2018. Some biologists recommended a shorter duration of 2–3 months to minimise the gain/loss that occurs due to natural mortality and permanent movements into or out of the survey area during a study (Karanth 1995; Jackson et al. 2006) however, others have pressed for an extended survey in order to capture more data, maximise the accuracy and improve the confidence for a closed population (Simcharoen et al. 2007; Wang and Macdonald 2009). Our camera-traps were not distributed in a grid pattern, which is also recommended to maximise accuracy (Tobler et al. 2008). This was difficult to achieve in our study areas because of accessibility and logistics. Local knowledge and expert opinions maximised the number of captures and increased the chances of individual identification. It is crucial to identify trails that leopards may use before placing the camera-traps, as this will maximise capture probability (Balme et al. 2009; Karanth and Nichols 1998).

It was difficult to obtain quality images of both sides of a leopard's flanks on paths narrower than 2 m in width. We were able to match sharply defined pelages on the hind limbs and dorsal tail surface of each individual, which increased our precision when using CMR analysis in a single estimate for a given population (Alonso et al. 2015). The common leopard also changes the shape of its rosettes with the movement of its body and its orientation to the camera-trap. We found that setting the camera at an angle of 45° to the track obtains clear spots and rosettes from the hind limbs or dorsal surface of tail, for individual identification. We identified individuals by comparing photos of each individual to other leopards and photos with clearer patterns were considered for comparison for individual recognition.

We are confident of our ability to identify individual leopards from photograph images and to capture histories obtained from camera-traps. We believe that cameratrapping is a viable tool for estimating the common leopard population size by maximising capture probability by placing camera traps at the *priori* identified hotspots located prior to the placement of camera-traps. Mixing probability estimates (Averaging effect from combining different models) suggested little evidence of heterogeneity as the estimate for pi is essentially 1, which we suggest was due to the small sample size.

The abundance estimates obtained from the data collected during the two years of camera-trapping, are 16–24 leopards in 2017, and 7–12 in 2018. Rather than a large decline in population between the years, we think it is likely that the population has remained the same. While there were fewer captures in 2018 (71 vs 121) there were also far fewer clear images that allowed individual patterns to be identified (46% vs 71%).

If, for example, the identification rate in 2018 had also been 71% then this would have estimated a population of 12–18, which falls within the range of 2017.

We are not sure why there was an absolute change in leopard images captured between the years. The difference may have been a result of a change in individual movements around their territory or possibly due to weather. There were drought conditions in 2018 compared to 2017 (Pakistan Metrological Department). Drought conditions may have affected the prey density in the study areas, forcing leopards to extend their home range in search of prey and hence lowering the detection probability for the camera traps. Typically, studies have found little difference in the overall travelling of leopards in different seasons (Mizutani and Jewell 1998; Dickman and Marker 2005), but there has been no research on the effects of an atypical season.

The frequency of capturing a leopard on the same track may be different depending on the size of the home range (Smith 1978; Silver et al. 2004; Rozhnov et al. 2015). For example, a leopard that is captured twice a week on a track may have a smaller territory than a leopard captured once a fortnight (Personal communication). However, most studies show that home range size varies in leopard among sexes. For example, females around birthing time (Rozhnov et al. 2015) and the location of female for male home range size (Bailey 1993; Odden and Wegge 2005). There is a possibility that the decline in population was real and may be due to the killing of leopards by poachers or unreported retaliatory killings. The total number of unreported killings may skew the number from 2.8 per year to a much higher number, as we did find signs of hunting from our field surveys and camera-trap data. Another possibility could be the sampling technique, such as moving a camera trap to an adjacent location over a short time frame, which means we could have missed out leopards in that area in the second survey.

The density of leopards in our study area, at 8–12 and 3.5–6.5 leopards/100 km², is more or less similar to other CMR such as 13–14/100 km² in India (Harihar et al. 2009). 3–9 leopard /100 km² in India (Athreya et al. 2013), Nepal (Carter et al. 2015), Cambodia (Gray and Prum 2012) Other studies have yielded relatively fewer leopards, such as 5/100 km² in Bardia National Park, Nepal (Wegge et al. 2009) and 3–4 leopards/100 km² in Mondulkiri Protected Forest Cambodia, and Manas National Park Assam, India (Balme et al. 2009; Borah et al. 2013). The mean encounter rate of females was higher than males on individual trails, perhaps indicating that males have larger home ranges than females (Morten and Per 2005).

This study confirmed the presence of leopards in the Swat and Dir and Margalla Hills despite the fact that the local people and the local wildlife department believe that the species had disappeared from the area. There is no record of livestock depredation and retaliation by villagers in close vicinity to the forest area. Interviews with nomads did confirm the depredation in the summer seasons. However they were unsure about the actual cause of those depredations, yet the details described were similar to that of the leopard predation (e.g. bite marks, dogs missing, etc.). The nomads travel from the plains to the hills during the summer in order to find fresh pasture on which to graze their herds. They keep the livestock in the open area overnight and are more vulnerable to leopard predation. We recorded higher capture probabilities, 0.10 to 0.20, according to the model selected based on AICc weight p(.), than reported for leopards in other studies, e.g. 0.04 (Wang and Macdonald 2009) and 0.02-0.10 (Borah et al. 2013) for similar habitats and this might be due to the identification of areas of high leopard use with the questionnaire survey.

Another approach used for estimating leopard density by Balme et al. (2009) was to try to fit trail count data (n = 39 sites) to single-season models where each pair of rows represented a unique trail where the camera-trap was later installed. Unfortunately, we did not have enough replicates for each trail, and we often observed the same leopard on several trails (using their unique rosette patterns), which would overestimate the density of leopards in the study area. Therefore, we did not rely on the trail count data in our capture analysis. Camera-trapping is more effective if the cameras are equally distributed, and cover a large area and identify each individual captured, but this is hard to achieve in rugged terrain and with animals from large home ranges (Tobler et al. 2008).

Leopards in Pakistan are sparsely distributed throughout the country (Sheikh and Molur 2004; Henschel et al. 2008; WWF-Pakistan 2014) and, hence, extensive sampling efforts and financial resources are required to cover the entire area to obtain sufficient information about their populations. One of the important outcomes of this research is to prioritise focusing on leopard hotspots from camera trap surveys, as they are a cost effective method for MARK-recapture analyses. To date, the abundance of leopards in Pakistan (Gallies, Swat, Dir, and Murree) has been anecdotal. The information about movement patterns and their dispersal behaviour is a conservation concern for many carnivores (Kanagaraj et al. 2013).

We observed that leopards use the Guzara Forest around the reserve areas extensively as a part of their home range. Based on information obtained from the Wildlife Department Khyber Pakhtunkhwa and WWF-Pakistan, 70% of the leopards that were killed by humans for revenge were outside the reserve area (Guzara Forest) and near the villages, and mostly during the winter season (Personal communication). The Guzara Forest received comparatively less snow in the protected areas, which may explain why leopards were more likely to be found there in winter and close to human settlements (Personal communication.).

Conservation efforts should focus more on hotspots identified in the Guzara Forest surrounding the Reserved Forest as this may reduce human-leopard conflicts. These forests allow leopards to extend their movements while searching for food. This extension also occasionally led to livestock depredation by leopards and resulted in the revenge killing of the leopards. Immediate compensation for losses of the livestock owners and a comprehensive awareness raising programme for schoolchildren together with the other members of the local community may significantly reduce the conflict between humans and leopards.

Some schools are located near those observational area and children travel through these routes to reach schools. Random attacks by leopards on children sometime create a stressful situation for children. Avoiding leopard trails during dawn and dusk can minimise the chances of such attacks.
We strongly recommend using a modified version of our protocol, in regions and areas where the presence of leopard populations is ambiguous. Our study suggests that camera-trapping, combined with a MARK-recapture method, can be useful for estimating the abundance in leopard habitat over time given the maximum number of individuals identified. Locating the remaining leopard population needs to be a high priority as this will, then, allow a focus on other conservation issues for this species.

The ultimate threat to the leopards and their occurrence in this habitat is extensive legal and illegal hunting activities. The Wildlife Department has issued numerous licences to locals for hunting the birds as part of the revenue generation programme. If a person is reported for illegal hunting, they are subjected to a low-value penalty and then re-issued with a licence. Then a person can effectively hunt anything since there are no checks and balances. Illegal hunting has created a disturbing condition for leopards that push them away from relative habitats. The other threats to leopards in this area are habitat degradation, unplanned infrastructure development, encroachment by humans, and an alarming use of the natural prey base.

Despite the limitation of camera placement in a grid, this camera-trap study provides the first evidence of the species presence in this area. The design method provided a reasonable way of estimating p (capture probability in this case) and we maximised the likelihood of capture by identifying hotspots. The mark recapture framework presents an advantage, as the individuals are identifiable from their unique pelage pattern. Although our method cannot provide absolute certainty with regard to abundance, we believe that the estimate we obtained from Mark provides a high degree of confidence when compared with actual field data of (identified individuals). However, to develop a sound conservation plan additional camera-traps studies on natural densities, habitat and the associated threats are needed in this region.

In conclusion, this research provides baseline information for leopard conservation and the mitigation of human and leopard conflicts for the Gallies and Murree Forest Division. The hotspots can be used to monitor population trends and any demographic changes through time. We also recommend future studies in different seasons and for longer periods. Our study suggests that the most productive conservation efforts may be beyond the protected area with special consideration given to those corridors (Guzara Forest) to ensure the long-term viability of leopard populations.

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RESEARCH ARTICLE



Performance of detection dogs and visual searches for scat detection and discrimination amongst related species with identical diets

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Abstract

Ecology often faces the problem that many threatened species are highly elusive but also conflict-laden. Thus, proper monitoring data are inevitable for their conservation and management. Indirect monitoring through scats is frequently used for such species, but scats of related species or species with similar diet are often visually indistinguishable. Since genetic methods for species identification are time-consuming and cost-intensive, a verification of the target species beforehand would be extremely beneficial in reducing effort to the analysis of the target species only. Such species discrimination could be provided through species-specific scat detection dogs. Therefore, we evaluated the reliability of species-specific scat detection dogs for two mustelid species feeding on identical diets: the Eurasian otter (*Lutra lutra*) and the American mink (*Neovison vison*), both of which are conflict-laden and increasing their populations and distribution ranges in central Europe. Their scats resemble each other in morphology and odour, exacerbating the differentiation even for experts. To evaluate whether detection dogs can reliably discriminate between related species feeding on similar diets and if their use would be beneficial, we tested their abilities against those of humans.

We first proved that scat characteristics are not statistically different between species. Likewise, visual species identification through people with different experience levels was only partly successful. Experts showed higher average accuracy (0.89) than non-experts (0.72 and below), but detection dogs (4 dogs) were able to discriminate otter and mink scats under laboratory conditions with an accuracy of 0.95. Moreover, otter scat detection dogs found up to four times more scat samples in the field, were twice as fast as human searchers and found an almost equal number of scats with different characteristics, while humans mostly found older and larger scats placed on hotspots. We conclude that using detection dogs for species identity will allow subsequent laboratory analyses to be species-specific and avoid spending time and money on laboratory work of the wrong species. It also provides more precise and unbiased information about the target species.

Keywords

American mink, Eurasian otter, *Lutra lutra, Neovison vison*, scat detection dogs, scat identification, species monitoring, wildlife detection dogs

Introduction

Many animal and plant species of interest in nature conservation are hard to find and therefore difficult to monitor. This is especially true for elusive or nocturnal species as well as for other species that are hard to capture. Combined with the fact that many elusive species are threatened or endangered and conflict-laden at the same time (Henle et al. 2013), it is even more challenging to analyse these species' distributions or population statuses, securing their conservation and management. Therefore, species monitoring is often realised indirectly through visual scat monitoring (MacKay et al. 2008). However, scat samples of related species or species with similar diets often cannot be differentiated morphologically (Davison et al. 2002, MacKay et al. 2008). This implies that monitoring, relying on scat only, could overestimate the presence of the target species unless determined genetically. Since genetic methods are timeconsuming and cost-intensive, a verification of the target species beforehand would be extremely beneficial in reducing effort to the analysis of the target species only.

Species discrimination can be provided using specially trained scat detection dogs, which are increasingly used for a reliable monitoring in nature conservation (see Mac-Kay et al. 2008, Dahlgren et al. 2012, Long and MacKay 2012, Woollett (Smith) et al. 2014). In previous studies, dogs successfully distinguished sympatric, closely related species [e.g. black bear (*Ursus americanus*) from grizzly (*U. arctos*) (Hurt et al. 2000, Wasser et al. 2004); kit fox (*Vulpes macrotis mutica*) from red fox (*V. vulpes*) and coy-ote (*Canis latrans*) (Smith et al. 2003); and bobcat (*Lynx rufus*) from red fox, grey fox (*Urocyon cinereoargenteus*), kit fox, domestic dog (*C. familiaris*) and coyote (Harrison 2006)]. While the diets of the abovementioned sympatric species partially overlap, to our knowledge, dogs have never been systematically tested to discriminate between related species feeding on an almost identical diet.

One such example is the syntopic occurrence of the threatened Eurasian otter (*Lutra lutra*) and the invasive American mink (*Neovison vison*) in Central Europe. A substantial proportion of both species' diet can consist of commercial fish (Geidezis 1996, Jedrze-

jewska et al. 2001, Poledníková et al. 2013), making them highly conflict-laden species (Kranz 2000, Kruuk 2006, Klenke et al. 2013). Since their populations are increasing in Central Europe (Kranz 2000, Hauer et al. 2009, Klenke et al. 2013, Poledníková et al. 2013, Lampa et al. 2015), the potential for human-wildlife-conflicts is increasing as well and proper species monitoring is essential (Poledníková et al. 2013). For otters, the standard monitoring method is non-invasive population monitoring with scats (Mason and Macdonald 1987). However, scat samples of otter and mink are often similar in shape, colour, and odour. In fact, most mink scats, visually identified as otter scats, contained fish remains and did not smell like typical mink scats, such that even experts could not differentiate between both (Lampa et al. 2015). Genetic capture-recapture methods have already been performed throughout Europe (e.g. Arrendal et al. 2007, Hájková et al. 2009, Bonesi et al. 2013, Lampa et al. 2015). For example, between 2006 and 2008, only 3–5% of all potential otter scats collected in the Upper Lusatia, Germany, could be conclusively genetically assigned to syntopic mink individuals and, from 2010 to 2012, this number has increased up to 20% (Lampa et al. 2015).

Given the discrimination abilities of trained detection dogs, we evaluated the reliability and benefit of species-specific detection dogs in species monitoring using the Eurasian otter and American mink. Specifically, we systematically tested the accuracy and precision of detection dogs and humans for discrimination between related species, even when individuals were fed the same diet. Secondly, we compared relative and absolute detection abilities of dogs and humans under field conditions.

Materials and methods

Collection and comparison of Eurasian otter and American mink scat

To compare otter scat and otter-like mink scat (herein referred to as "mink scat"), we used the data from a previous otter monitoring study of the Upper Lusatian Heath and Pond Landscape in eastern Saxony, Germany (see Lampa et al. 2015 and Suppl. material 1: S1.1 for a description of the study site and sampling design). To investigate whether otter and mink scats differed in their characteristics (amount, colour, sliminess, exposure), we used Pearson's chi-squared test. If the test was significant, we used pairwise chi-squared tests and the Bonferroni-Holm correction for p-values as a post-hoc test (Holm 1979).

Additionally, we obtained scats from captive otter and mink from the otter centre Hankensbüttel (http://otterzentrum.de). In April 2015, eight Eurasian otters (4 males, 4 females) and four mink (all males) were fed the same fish species only for two weeks. After three days of digestion adjustment, three scat samples were collected per species per day for ten days, labelled according to the potential individuals and frozen immediately. A total of 60 frozen scat samples divided into three to five partial samples each were stored in separate, airtight plastic tubes. To determine the difference in scat colour between both species when fed on an identical diet, we performed Fisher's exact rank test using 20 random otter and mink samples.

Detection dogs and training

Dogs used in this study were privately-owned pet dogs. We trained two dogs to detect otter scats only. For comparisons, we trained two additional dogs to detect mink scats only (Table 1). We used positive reinforcement without coercion. While three dogs were already plant detection or rescue dogs, the youngest one had no previous experience. All dogs first performed lab tests (see below) on a scent box (Fig. 1). The scent box, constructed of a cardboard, had five holes with a centre-to-centre distance of 30 cm to ensure scent overlap (McKay 2014). Five plastic cups could be placed into the scent box deep enough that the handler could not see whether the cup contained any-thing. Additionally, the cups were equipped with a lid with three small holes. We used the systematically collected scats from captivity for training and testing on the scent box to ensure that individuals were fed on an identical diet.

All dogs were trained on scat scent following Wasser et al. (2004). For each training day, scat samples needed were defrosted, used for training and subsequently refrozen. For imprinting, i.e. focussing a dog on its target scent, we used mixed samples of four individuals of the target species (Kerley 2004). We chose a passive alert (sitting) that involves no barking, scratching or pawing to keep the influence on targets and wildlife in later field deployments as low as possible (DeMatteo et al. 2019). For applications in field-work, we also added a "show-me" command where the dog pointed to the specific scat to be able to detect hidden scats and species-specific scats on hotspots (defined as minimum three scats in less than 15 cm distance).

In contrast to Wasser et al. (2004), the dogs were not guided along the scent box, but allowed to walk along independently for three times at a maximum upon a "search" command (Kerley 2004) (Fig. 1). Each correct finding was quickly rewarded with food. Dogs were allowed to play with their toy following several trials before they got a break. After the dogs were habituated to the scent box and trained on their target scat, we performed a pre-test to examine that the dog had understood his task (Suppl. material 1: S1.2). When the dog passed that test without an error, species discrimination training started. We used the method of errorless discrimination (Gadbois and Reeve 2014) to train the dogs alert at otter but ignore mink scat, while the mink scat detection dogs alert at mink but ignore otter scat (Suppl. material 1: S1.2). Then, the final discrimination test followed (see below).

Once the detection and discrimination were working properly indoors, we started the field training of the otter scat detection dogs. We did not train the mink scat detection dogs in the field since the overall goal was to improve necessary otter monitoring. Searching took place without a leash such that the dog would not be biased towards a particular direction by the handler (MacKay et al. 2008, Woollett (Smith) et al. 2014). At the beginning of field training, the handler knew locations where the target and non-target scats were hidden so that the dog could be rewarded immediately. Subsequent trials were conducted blind as illustrated in Fig. 2.

Throughout field training, the dogs were confronted with various surfaces (short or tall grass, understorey, debris, logs, concrete) and elevations (level to steep) and trained at different temperatures (-5 °C to 32 °C), precipitation (sunny, cloudy, drizzle, rain-

Dog	Bagheera	Zammy	Cue	Zoey
Age	8 years	1 year	8 years	4 years
Breed	Australian Cattle Dog Mix	Border Collie	Border Collie	Border Collie
Origin	animal shelter	breeder	breeder	breeder
Previous experience	plant detection dog	none	certified rescue dog	certified rescue dog
Target species	Eurasian otter	Eurasian otter	American mink	American mink
Handler	AZ	AGS	LH	LH

Table 1. Overview of the scat detection dogs used in this study. Ages refer to the tests in 2017 and not to the start of the training.



Figure 1. Searching along the scent box (left) and alerting at the target scat (right), taking the example of the otter scat detection dog Zammy.

ing, snowing) and wind conditions (none to severe). To enlarge the dogs' scent range, we used genetically verified scat samples of male and female otters from the Upper Lusatia additionally to the samples from captivity. After both dogs were able to detect all otter and ignore all mink scats in ten subsequent blind trials, whereby each trial contained 1–2 otter and 1–2 mink scats, we also took the dogs to areas where Eurasian otters but no American minks were present to mimic field conditions and verify whether the dogs would alert on wild scats. We obtained permission from pond farmers and local game authorities for all pond areas where we conducted field training.

Species discrimination tests

We assessed human and dog abilities to discriminate between otter and mink scats using 20 random captive scat samples of different otter and mink individuals all fed with fish only. By chance, eleven samples belonged to otter and nine belonged to mink. The 20 samples were unknown to both humans and dogs. Every test person and every dog got the same samples for comparability. Neither test persons nor handlers knew how many samples belonged to which species.

Test persons were classified according to their expertise into beginner (person has never worked with scats of otters or minks or just started, i.e. total hours in the field: 0–72), experienced (person has already searched for at least one species, i.e. total hours in the field: ca. 240–336) and expert (person has already searched for both species intensively,



Figure 2. Chronology in the field training of the scat detection dogs, taking the example of the otter scat detection dog Bagheera. (1) A field assistant hid the scat using laboratory gloves and (2) walked through the search area a few times in order to cover up tracks out of sight of the handler. (3) Ritualised, the dog sat in front of the handler and the target scent was presented to the dog in a tube. (4) The dog was sent to search the area independently and (5) gave a passive alert (sitting or lying down, depending on the dog's preferences) in front of the scat found. (6) We requested the command "show me" where the dog indicated precisely the source of scent through freeze-and-stare but was carefully trained not to touch the scat. The assistant would then indicate the handler whether this find was correct. (7) For each correctly found scat, the dog would be rewarded with a valuable treat (e.g. dried meat or favourite toy). Wrong alerts would be commented with "wrong" and the search would start again.

i.e. total hours in the field > 840). Test samples were presented in plastic cups in a 4×5 grid (Fig. 3) and test persons were asked to assign each scat sample to either otter or mink. To obtain which parameters influenced correct species assignment of a scat, we performed a generalised linear mixed model (GLMM) with "1" implying correct and "0" incorrect assignment using a binomial error distribution. Explanatory parameters were tested for non-collinearity and include the species, sex, the day sampled reflecting the time since digestion adjustment, colour and mass of the scat, expertise and the random intercept of the person's ID. We obtained parameter significances by means of a likelihood ratio test (LRT) of the full model against the model without the parameter in question and overall model significance using an LRT of the full model against a model including the random term only. Since humans assigned the species mainly visually, we further analysed whether test candidates used the scat colour for species assignment (Suppl. material 1: S1.3).



Figure 3. Setup for human scent discrimination test.

To ensure a standardised testing procedure between dog and human abilities, we used the scent box for final discrimination tests with dogs (Fig. 1). We created test protocols with 20 random trials. Each trial contained one cup with an individual otter scat and one cup with an individual mink scat as well as three blanks (Suppl. material 1: S1.2). We ensured that each of the 20 test samples was used at least once. The target and non-target species were correctly assigned if the dog alerted to or ignored that cup, respectively. All tests were conducted double-blind (Suppl. material 1: S1.2).

For both human and dog species discrimination tests, we calculated the sensitivity as the amount of true-positives (target samples correctly assigned) divided by the total number of all target samples and the specificity as the amount of true-negatives (nontarget samples correctly assigned) divided by the total number of non-target samples. We further calculated the accuracy (validity) as the amount of all true-positives and true-negatives divided by the total number of target and non-target samples presented and the precision (reliability) as the amount of true-positives divided by the total number of positive responses (all alerts for dogs or all otter assignments for humans). We refer to a target sample as otter scat for humans and otter detection dogs, but mink scat for mink detection dogs and a non-target sample as mink scat for humans and otter detection dogs, but otter scat for mink detection dogs.

Field procedures in the Upper Lusatia

In March 2017, we conducted a five-day otter monitoring in the Upper Lusatia in the study area of Lampa et al. (2015) where both otter and mink occur (see Suppl. material 1: S1.1). Our overall aim was to compare visual and detection dog searches for wild otter

scat under field conditions. Since both cleared and uncleared transect monitoring is regularly used for otter monitoring, we applied both methods. We thus divided the monitoring season in one day for clearance of four pre-defined transects where all scats found visually were removed, two days to compare the abilities to detect freshly deposited wild otter scat from the night before on the pre-defined transects amongst teams and two days for otter presence monitoring on uncleared transects at ponds nearby. Transects followed trails along ponds in four pond areas: "Biwatsch", "Entenschenke", "Mühlteich", and "Langner". They were characterised by a starting point and direction (Suppl. material 1: S1.1, Fig. S1). Vegetation was comparable amongst transects and consisted mainly of low grass and trees. "Biwatsch" also contained a substantial amount of bushes.

We allowed two hours for clearance but only one hour in the comparisons amongst teams (see below). We always applied time and not length restrictions to allow each team to search at its appropriate speed. We had two human teams, consisting of one expert and two students or one experienced person and three students and two otter scat detection dog teams, each consisting of one experienced handler, one student orienteer and one otter scat detection dog (Table 2). All students were introduced to otter scat detection on the first day.

Relative detection abilities

Each of the four teams visited the four previously cleared transects independently without exchange of people or knowledge. We used a rotation design, meaning that each team was once the first, second, third or fourth team on one transect. We limited the time spent on each transect to one hour so that each team could reach individual end points. Each team marked the start and end points to calculate transect lengths, as well as localities of otter scats on a plane-table sheet. For each scat found, the team described the site (on litter, on log, on rock, in bush, buried, den, latrine, other), scat condition (fresh, mostly fresh, dry, decayed), colour (yellow, green, black and all combinations thereof) and exposure (not exposed, exposed on natural structures, exposed on human structures) and estimated the scat size or gave the number of scats in the case of a hotspot. Each team also took two photos per scat, one close-up and one including the surroundings. These photos were used to assess whether the scats found by different teams were identical or different amongst search teams. During otter presence monitoring outside transects, protocolling was identical but no time and space restrictions applied. Dog teams additionally evaluated dog performance (Suppl. material 1: S1.4) and the likelihood of finding that scat without a dog (very low, moderate, high, uncertain).

We then analysed how many scats were found by each team per hour, the distance reached per hour and whether scat characteristics differed between scats found by human and dog teams using a t-test for count data and chi-test for categorical data. Data outside transects (presence monitoring) were only compared quantitatively since monitoring took place in different pond areas with different accessibilities and otter abundances.

Absolute detection abilities

The total number of otter scats was unknown throughout the field tests. Therefore, we estimated the total number of otter scats per transect using two independent visits of dog teams and the photos to assess which of the observed scats were "recaptures". Likewise, we estimated the total number of otter-like scats per transect, which comprises both otter scats and misidentified mink scats, using two independent visits of human teams. We calculated the minimum number of misidentified mink scats as the difference between the total number of otter and otter-like scats. Since we expect human teams to generally overlook very small or hidden scats (Long and MacKay 2012, Bonesi et al. 2013), the estimated total number of otter scats, based on human samples, would be smaller than that based on dog samples. Thus, if the estimated number of otter-like scats is larger than otter scats, the difference between both can only refer to a minimum number of misidentified mink scats.

We applied the Lincoln-Petersen estimator with the Chapman correction for small sample sizes (Seber 1982) using photos together with site descriptions for individual identification of scats. We shortened transects to the maximum common distance surveyed amongst all teams. We then calculated the detection rate for human and dog teams. All statistical analyses were conducted using R (R Core Team 2018) and the R-packages *exactRankTests* (Hothorn and Hornik 2013), *fifer* (Fife 2017) and *lme4* (Bates et al. 2015).

Results

Comparison of Eurasian otter and American mink scat

We found no combination of scat characteristics in wild samples of otter (n = 1273) and mink scats (n = 161) that would clearly indicate the species. Both species used hotspots and sometimes hotspots even contained scats of both species. However, otters used significantly more hotspots amongst all scats found (41%) than minks (23%) (χ^2 test, $\chi = 6.6$, df = 1, p = 0.01). Likewise, otters used significantly more exposed surfaces (χ^2 -test, $\chi = 45.22$, df = 5, p < 0.001) despite all surfaces being used by both species. The amount of scat (χ^2 -test, $\chi = 0.06$, df = 2, p = 0.97) and the sliminess (χ^2 test, $\chi = 0.95$, df = 2, p = 0.62) were not different between both species. We recognised the same amount of jelly scats ($\approx 20\%$) for both species, but while one-third of them were yellowish for both, the rest were greenish for minks and half greenish, half reddish for otters (χ^2 -test, $\chi = 50.57$, df = 2, p < 0.001).

Of the scat samples from captivity where both species fed on the same fish, we found that, of the otter scats, 18% were dark-green, 55% green, 18% yellow-green, and 9% yellow. Of the mink scats, 33% were black, 22% dark-green, 11% green, 22% yellow-green and 11% yellow. There was no statistical difference in scat colour between species (Fisher-test, df = 4, p = 0.11).

Species discrimination tests

We tested 3 beginners, 3 experienced persons and 4 experts. We found that the species assignment for the beginners were rather random with average accuracy of 0.58 (sensitivity from 0.45–0.64, specificity from 0.33–0.78) and average precision of 0.63. Experienced persons obtained an average accuracy of 0.72 (sensitivity from 0.63–0.81, specificity from 0.56–0.78) and an average precision of 0.74. Experts reached an average accuracy of 0.89 (sensitivity from 0.81–1, specificity from 0.67–1) and an average precision of 0.89 (Suppl. material 1: S1.5, Table S2). The overall average accuracy and precision were 0.75 and 0.77, respectively. The highest accuracy reached was 0.95.

None of the scat characteristics [species (p = 0.43), sex (p = 0.06), day sampled (p = 0.08), colour (p = 0.89), mass (p = 0.41)] clearly influenced correct assignment, with the almost significant sex-parameter being due to a male-biased sample and the almost significant day-sampled-parameter reflecting that the longer the species fed on fish only, the higher the chance of correct assignment. The colour was not significant because persons were assigning the species to different colours (Suppl. material 1: S1.3). However, the expertise of a test person clearly explained the assignment (p = 0.004), leading to an overall significant GLMM (p = 0.04). Correct assignment increased strongly with experience level.

In comparison, the four detection dogs showed average accuracy of 0.95 (from 0.9–1) with a sensitivity of 1 for all dogs and average specificity of 0.97 and 0.83 for the otter and mink scat detection dogs, respectively (Suppl. material 1: S1.5, Table S3). This resulted in average precision of 0.97 and 0.85 for the otter and mink scat detection dogs, respectively.

Relative detection abilities

Results per team and transect are given in Table 2. Otter detection dog teams found significantly more scats per hour (paired t-test, one-sided, t = 4.25, df = 7, p = 0.002, mean difference = 4.5 scats per hour) and were significantly faster (paired t-test, one-sided, t = 2.33, df = 7, p = 0.02, mean difference = 0.25 km/h) on standardised transects than human teams (Fig. 4). On average, dog teams found 12.5 and 13.5 scats per hour (paired t-test, two-sided, t = -0.48, df = 3, p = 0.66), but the team with the experienced dog Bagheera was slightly faster (1.1 km/h) than the team with the recruit Zammy (0.9 km/h) (paired t-test, two-sided, t = 3.27, df = 3, p = 0.05). The two human teams found eight and nine scats per hour on average (paired t-test, two-sided, t = -0.41, df = 3, p = 0.60), respectively. During otter presence monitoring outside transects, dog teams were still faster (0.6 km/h vs. 0.4 km/h) and found more scats per hour (8.8 scats/h vs. 5.5 scats/h) (Table 3).

On standardised transects, human and detection dog teams found a total of 64 and 104 scats (Table 2). Of the scats found by each team, significantly more scats belonged to hotspots in the human (41%) than in the dog (25.7%) sample (χ^2 -test, $\chi = 4.6$, df = 1,

Members	Transect	Distance reached [km]	Scats found	Scats per maximum common distance
Bagheera, AZ,	Biwatsch	1.12	12	5
1 student	Mühlteich	0.41	15	9
	Entenschenke	0.98	13	13
	Langner	1.36	10	3
Zammy, AGS,	Biwatsch	1.06	10	5
1 student	Mühlteich	0.36	22	12
	Entenschenke	0.80	13	12
	Langner	1.24	9	3

3

10

13

3*

4

20

8

3*

Table 2. Results for transect comparisons amongst search teams. Time spent on each transect was limited to 1 h.

Team

Dogs1

Dogs2

Humans1

Humans2

Expert, 2

students

Experienced

person, 3

students

Biwatsch

Mühlteich

Entenschenke

Langner

Biwatsch

Mühlteich

Entenschenke

Langner

* Those three scats were found by both human teams at the beginning of the transect behind a thorny bush. The search of the dog teams started after that thorny bush so that the dogs could not pass them.

1.06

0.20

0.68

0.57

0.71

0.52

0.84

0.80

Table 3. Scat parameters evaluated for scats found by human teams and dog teams on standardised transects and during otter presence monitoring outside transects, with ranges given in brackets. Scat conditions do not add up to 100%, as on hotspots occasionally, several conditions could be found which are not included here.

Parameter	Human teams		Dog teams	
_	transect	outside transect	transect	outside transect
Scats / hour	8.5 [3-20]	5.5 [1.3–10]	12.6 [9–22]	8.8 [5.2–12]
Km / hour	0.7 [0.2–1.1]	0.4 [0.2-0.6]	1 [0.4–1.4]	0.6 [0.5-0.7]
Scat condition	35% dry / decayed,	73% dry / decayed,	36% dry / decayed,	48% dry / decayed,
	61% (mostly) fresh	22% (mostly) fresh	54% (mostly) fresh	42% (mostly) fresh
Scat size	61.8% large, 30.9%	50.7% large, 34.2%	32.6% large, 39.8%	41% large, 34.6%
	medium, 7.3% small	medium, 15.1% small	medium, 27.6% small	medium, 24.4% small
Hotspots	41%	31.5%	25.7%	25.3%
Exposure	81.4%	79%	not evaluated	not evaluated

p = 0.03) and significantly more scats were large in the human (61.8% large, 30.9% medium, 7.3% small) than in the dog (32.6% large, 39.8% medium, 27.6% small) sample $(\chi^2$ -test, $\chi = 21.96$, df = 2, p < 0.001) (Table 3). During otter presence monitoring outside transects, scats found by human teams were preferably older and larger and belonged more often to hotspots. No such bias was detected for the scats found by dog teams, which found almost equal numbers of different sizes, ages and amount (Table 3). The likelihood of finding a specific scat without a detection dog was high in 22.5%, moderate in 31.7%, low in 39.4% and uncertain for 6.4% of the scats. Dogs showed high working abilities for their jobs and no change in their performance across time (Suppl. material 1: S1.4).

2

10

13

0

3

12

7

0



Figure 4. Comparison on the abilities of dog and human scat detection teams on standardised transects. The number of scats refers to the number of otter scats for detection dogs and otter-like scats for human teams.

Absolute detection abilities

Scat photo-identification performed well on one transect ("Mühlteich") with almost exclusively "naturally exposed" scats combined with scratch piles. Each team detected between 9 and 12 scats (Table 2) and the likelihood of finding a scat without a dog was almost always estimated as moderate to high. Average detection rate for detection dog and human teams was 0.60 [confidence interval (CI) 0.47–0.82] and 0.48 [CI 0.35–0.78], respectively. We estimated an abundance of 17.6 [CI 12.8–22.4] true otter scats and 22.8 [CI 14.1–31.6] otter-like scats. Thus, we assume that a minimum of 5 scats (22% [CI 9.2%-29.1%]), visually identified as otter, belonged to mink.

On two further transects, the relative detection rate for dog teams was 3–4 times higher than that of human teams (Table 2), making an estimation of scat abundances amongst all teams impossible. We therefore estimated scat detection rates within the maximum common distance for dog teams only and for human teams only. Detection rates for dog and human teams were estimated as 0.72 [CI 0.60–0.89] and 0.43 [CI 0.26–1] at "Langner" and 0.40 [CI 0.26–0.84] and 0.21 [CI 0.10–1] at "Biwatsch", respectively. Confidence intervals for the human samples should be treated with caution due to the very low sample sizes and extremely low "recapture" rates. On the fourth transect ("Entenschenke"), photo-identification failed due to otter scats being mostly on hotspots.

Discussion

In many parts of Europe, the Eurasian otter and American mink co-exist syntopically without out-competing each other (Harrington et al. 2009, Klenke et al. 2013, Lampa et al. 2015). When monitoring syntopic or sympatric species, scat differentiation is ex-

tremely valuable. As expected, we could not detect differences between characteristics of otter and mink scats that could be used for visual species identification. We detected more hotspots and more exposed scats for otters than for minks. However, Lampa et al. (2015) found fresh mink and otter scat on the same marking sites, making visual species assignment in the field impossible. Importantly, since mink scat was only sampled when identified as otter, results only represent the otter-like mink scats and might not reflect the overall use of hotspots and exposed areas in minks. Scats from minks that fed on other diet items, such as birds or small mammals, can easily be identified through remains of bones, hairs, feathers and a stronger smell and are thus not considered here. Rather, comparisons were intended to determine whether specific characteristics could be used for species identification when both species fed on identical diets, which is not the case. Without cross-checking species through genetic methods or detection dogs, a high number of otter-like scats of mink origin would significantly bias otter monitoring based on scat samples only (Lampa et al. 2015).

Often, scats of sympatric carnivores cannot be differentiated morphologically (Mac-Kay et al. 2008). Our results indicated that human searchers showed the same falsepositive detection rate in the field as in the species assignment test, which was comparable to an earlier study (Lampa et al. 2015). In other studies, even experts failed to reliably distinguish pine marten (Martes martes) scats from those of foxes (Vulpes vulpes) (Davison et al. 2002) or at detecting mink scat amongst other mustelid species (Harrington et al. 2010). Our species discrimination tests showed that beginners assigned the species randomly, while experts showed high accuracy nearly equalling the accuracy which dogs already showed during the discrimination training (Suppl. material 1: S1.2). Moreover, it took years to become an expert (given that the monitoring time per year is limited), while the training of detection dogs just needed a few months and was, thus, a much faster method. After completing discrimination training, detection dogs clearly outperformed the abilities of any expert. However, we suggest that dogs performing only one search task (e.g. wildlife detection) might reach higher accuracy faster, since each search task (e.g. being a search and rescue dog in parallel, as for our mink detection dogs) would require a huge amount of training simultaneously which is unlikely to be adequately addressed.

In comparison, Oldenburg et al. (2016) also tested specificity and sensitivity of one otter scat detection dog, but they used unrelated decoy species with entirely different diets. In their final test, the dog showed a sensitivity of 1, as ours did, but it also alerted at rabbits and hares with a specificity of 0.95, summing to an accuracy of 0.96 and a precision of 0.7. In other studies, scat detection dogs showed a specificity of 0.93 for fisher (*Martes pennanti*) (Long et al. 2007a) and 1 for kit fox (*Vulpes macrotis*) (Smith et al. 2001), stressing the high discrimination abilities of dogs. Hence, using detection dogs for species identity will allow subsequent laboratory analyses to be species-specific and avoid spending time and money on laboratory work of the wrong species.

Furthermore, our detection dog teams significantly increased the efficiency of field monitoring by detecting more scats and reaching a longer distance than human teams per hour. Moreover, detection dogs were twice as fast as human teams despite their handlers having to stop three to four times more often to protocol samples and fill out a longer protocol. In North America, Richards (2016) also compared the abilities of detection dogs with humans, both searching for the scat of the American mink and North American river otter (Lontra canadensis) simultaneously. On a 2.4 km shoreline transect searched for 2 h, an expert and a detection dog found one and eleven scats, respectively and, on another transect of 5.5 km length, a biologist could not detect any scat while detection dogs found 16. Likewise, Smith et al. (2001) reported that a detection dog found up to four times more kit fox scats than an experienced searcher. In addition, our dogs were less selective in the area they searched, as they detected scats on logs reaching into the water or below leaves and in grass impossible to detect visually. Finally, while humans detected scats with characteristics that increased their visibility (larger, more exposed, older and thus brighter), scats found by dogs were much less skewed towards a particular size or age. Scat sampling, biased to more exposed or larger scats, could bias ecological analyses (Birks et al. 2005, Bonesi et al. 2013). Thus, their ability to find many scats over large areas, including small and hidden ones and their lesser spatial and sampling bias, make detection dogs particularly helpful for studying marten species (Long and MacKay 2012). Typical problems when monitoring martens through scat monitoring, including biased searching ("knowing where to search") and scat differentiation (Birks et al. 2005), can be overcome by using detection dogs.

In this study, different detection rates of the detection dogs were likely due to different vegetation conditions amongst transects, with the lowest detection rate at the transect with many bushes. Nevertheless, detection rates of detection dogs were always twice as high as visual detection rates. In studies with other mammals, scat detection dogs also outperformed other monitoring methods, such as cameras, hair snares and scent stations (Harrison 2006, Long et al. 2007b, Tom 2012) and required much less time to ascertain species presence (Long et al. 2007a, Clare et al. 2015). Importantly, the frequency of detection and the accuracy can also vary amongst dogs, dog-handler-teams, day, weather and place (MacKay et al. 2008), despite variation can be limited with proper adjustments (Leigh and Dominick 2015). It is therefore necessary to adapt the training specifically to the dog and the given field conditions (Woollett (Smith) et al. 2014).

Conclusion

Using species-specific scat detection dogs is saving time during species monitoring and allows subsequent laboratory analyses to be species-specific. Even for related species feeding on identical diets, scat detection dogs showed highly accurate and precise species discrimination abilities, which outperformed those of experts. Detection dogs were also reliable in the field and more efficient than humans. Moreover, detection dogs provided more precise and unbiased information about the target species than visual searching through, for example, detecting hidden or very small samples. With proper training provided, their use is highly recommended for species monitoring through scats and will significantly contribute to optimal conservation of threatened and management of conflict species.

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Supplementary material I

Appendix S1. Additional information and analyses

Authors: Annegret Grimm-Seyfarth, Aleksandra Zarzycka, Teresa Nitz, Lisa Heynig, Nadine Weissheimer, Simone Lampa, Reinhard Klenke

Data type: statistical data

- Explanation note: S1.1 Original Eurasian otter monitoring study; S1.2 Detection dogs pre-test and discrimination training; S1.3 Do humans assign species based on color? S1.4 Evaluation of dog performance in the field; S1.5 Species assignments for humans and dogs.
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RESEARCH ARTICLE



Contrasting effects of altitude on species groups with different traits in a non-fragmented montane temperate forest

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Abstract

Temperature has strong effects on species composition and traits. These effects can differ within and between species groups. Thermoregulation and mobility are traits which can be strongly affected by altitudinal distribution. Our aim was to investigate the influence of altitude on the species richness, abundance and composition of species groups with different trophic, thermoregulatory and mobility traits. Carabids (Coleoptera; Carabidae), hoverflies (Diptera: Syrphidae) and birds (Aves: Passeriformes) were counted in three altitudinal belts with a total elevation difference of 700 m (from 300 m to 1000 m a.s.l.) in the same habitat type (non-fragmented temperate montane mixed beech and fir forest). We found that endotherms and more mobile species (i.e. birds) had a smaller turnover than ectotherms (i.e. hoverflies) and less mobile species (i.e. carabids), from which we can predict that the former species will undergo a less extreme shift than the latter in global warming scenarios. Species turnover across the altitudinal gradient increased from birds to hoverflies to carabid beetles. The effect of altitude on phenology was different between the studied ectotherm species groups (carabids and hoverflies). Hoverflies experience a phenological delay of species richness and abundance at higher altitudes in spring, but not at the end of summer, which implies that hoverfly phenology is affected by a change in temperature, while carabid beetle abundance exhibited a delay in phenology in summer at higher altitudes. We suggest that species that are expected to be most affected by climate change, such as ectotherms and species with poor dispersal ability should be prioritised as the best indicators for monitoring and conservation management purposes.

Keywords

climate change; Carabidae; Syrphidae; Aves; altitudinal gradient; species assemblage

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Introduction

Climate change has a dramatic effect on the geographical ranges of many plant and animal species (Parmesan et al. 1999; Hill et al. 2002; Wilson et al. 2007; Wilson and Maclean 2011). Not only are species ranges expanding or moving northwards, they are also shifting to higher altitudes (Konvicka et al. 2003; Wilson et al. 2007). Furthermore, there is evidence of phenological change in insect species earlier in the season (Stefanescu et al. 2003), which is because growth rate is directly related to temperature (Bale et al. 2002). There is increasing knowledge about the effect of climate change on different species groups over latitudinal (Chen et al. 2011; Devictor et al. 2012), as well as altitudinal gradients (Hill et al. 2002; Chen et al. 2009; Pizzolotto et al. 2014; McGrann and Furnas 2016).

Altitudinal gradients can be used as a model for future impacts of increasing temperatures on biodiversity (Botes et al. 2006; Korner 2007). Many patterns of biodiversity are dependent on altitude, with the gradual decreasing and the humpshaped relationships being the most commonly described (Rahbek 1995; Hodkinson 2005; Sanders and Rahbek 2012). Some of the underlying mechanisms for these patterns are source-sink dynamics (Kessler et al. 2011), geometric constraints (Rahbek 1995; Romdal and Grytnes 2007), disturbance (Bunn et al. 2010), evolutionary history (Machac et al. 2011), climate and productivity (Rahbek 1995; Wang et al. 2009) and species physiology (Žagar et al. 2018). A general negative metabolic response to temperature shifts was observed for high elevation specialists across vertebrate and invertebrate ectotherm taxa (Žagar et al. 2018). However, only a few abiotic parameters change gradually with altitude: atmospheric pressure, temperature and clear sky turbidity (Korner 2007). If the change is only measured in one habitat type, the direct effect of environmental temperature on animals can be determined (Bale et al. 2002; Tylianakis et al. 2008). Therefore, it is important to eliminate habitat change as a factor and take into account only the change in biodiversity across an altitudinal gradient in more or less homogenous and more or less non-fragmented habitat.

Although many different organisms have already been investigated for altitudinal distribution (Hodkinson 2005; Sanders and Rahbek 2012), they were all investigated in different habitats and regions (Sanders and Rahbek 2012). In butterflies, it was found that, due to climate change, the high altitude species and northern latitudinal species were going upwards to higher altitudes or latitudes (Wilson et al. 2007). Thus, the phenological window which was narrower on higher altitude may increase with climate change, because of warmer temperatures (Illán et al. 2012). Only a few studies have, however, considered species groups with different traits when studying biodiversity structure across an altitudinal gradient in the same habitat.

In this study, we investigated the influence of altitude and season on patterns of alpha and beta diversity and abundance of carabid beetles (Coleoptera: Carabidae)

and hoverflies (Diptera: Syrphidae) as ectotherms and passerine birds (Aves: Passeriformes) as endotherms in a mixed Dinaric beech and fir forest (Omphalodo-Fagetum s. lat.) in Central Europe. All of these groups are known to be good indicators for environmental and climate change (Furness and Greenwood 1993; Sommaggio 1999; Kotze et al. 2011; Pizzolotto et al. 2014). However, selected groups are very different in their mobile capabilities with forest species of carabid beetles being predominantly wingless with low dispersal power (Kotze and O'Hara 2003; Pizzolotto et al. 2016) and thus highly dependent on habitat connectivity (Jopp and Reuter 2005). It is well known that carabid beetle assemblages change rapidly due to environmental changes (Gobbi et al. 2015; Prass et al. 2017). We considered carabid beetles, which include high trophic species variability from predators, herbivores to omnivores (Lövei and Sunderland 1996), as a model group for low dispersal mode. As a model group for medium dispersal mode, we have selected hoverflies with all species in the assemblage having wings and being higher dispersers than carabid beetles, some species even being partly migratory (Odermatt et al. 2017). The hoverflies, as adult pollinators and as larvae, occupy a large radiation of niches, varying from plant feeding, predators, microbe feeders or saproxylic species. In many studies, they are shown to be sensitive to habitat disturbance in agricultural land, as well as forest landscapes (Sommaggio 1999; Gittings et al. 2006; Schweiger et al. 2007; Smith et al. 2009; de Groot et al. 2016). Passerine birds are known as the most mobile species group and were selected in our study as a model group for high dispersal mode. According to their good flight capabilities, the birds are able to exhibit longer distance seasonal flights and dispersal from few to some thousands of kilometres, shown to largely depend on their habitat specialism (Martin and Fahrig 2018). The forest assemblages of passerine birds mainly contain insectivore and granivore species (Snow and Perrins 1998).

First, we looked at the possible influence of temperature by comparing differences in diversity patterns between higher and lower altitudes, according to taxonomic groups in continuous non-fragmented forest area, to avoid the effects of habitat fragmentation. We then examined differences in the phenology of ectotherm insect groups with respect to altitude. The studied species groups can be differentiated on the basis of thermoregulation, mobility and degree of specialism. First, we expected ectotherms (carabid beetles, hoverflies) to exhibit greater dissimilarity across an altitudinal gradient than endotherms (birds), since the former is more affected by temperature during their life cycle (Žagar et al. 2018). Secondly, it is expected that species groups with greater dispersal ability, such as hoverflies, will exhibit a smaller change in assemblages than less mobile species, such as flightless carabid beetles (Steinitz et al. 2006). Thirdly hoverflies, which have high metabolic cost compared to flightless carabid beetles (Harrison and Roberts 2000), exhibit different phenology patterns across an altitudinal gradient because they are more dependent on temperature (Gilbert 1984).

Materials and methods

Area description

To study climate driven effects across an elevational gradient, we selected a continuous and non-fragmented forest area of Mt. Krim (45°58'N, 14°25'E), 10 km south of Ljubljana (central Slovenia), which is part of a continuous montane forest range, extending from Slovenia across the western Balkan Peninsula to Serbia. The area is 140 km², 77% of which is covered with forest and 20% of which is not forested, the remainder being urban areas (i.e. settlements) which are situated only in the lowlands. Mt. Krim is a medium altitudinal mountain in the North Dinaric Alps ranging from 290 to 1108 m a.s.l. The slopes are covered predominantly with mixed temperate forest of Omphalodo-Fagetum s. lat. in which beech (Fagus sylvatica) is the dominant tree species (36%). Other common tree species are silver fir (Abies alba) and Norway spruce (Picea alba). Most of the forest is in an old growth phase, with trees whose trunk diameters are more than 30 cm at breast height. Clearings are small and dispersed, mostly around the settlements (Vrezec 2003; Vrezec and Tome 2004). During the study, Mt Krim was studied on three altitudinal belts (low (300-550 m), middle (550-800 m) and high (800-1100 m). The sampling sites in altitudinal belts were chosen to avoid larger forest clearings and in such a way that they did not differ in type, age, tree species composition, including tree density/abundance, light and other environmental conditions and forest structure.

Survey protocol

Fieldwork was conducted in spring, summer and autumn of 2010. During this survey, the altitudinal distribution of three species groups was investigated: carabid beetles, hoverflies and passerine birds. These groups were investigated in the three altitudinal belts.

The carabid beetles were sampled with pitfall traps using vinegar as an attractant (Vrezec and Kapla 2007). A line of five traps at 20 m spacing was set in each altitudinal belt. The traps were set every month for five to seven days in April (19.4–26.4), May (15.5–21.5), June (18.6–23.6), July (21.7–28.7), August/September (28.8–4.9) and October (1.10–8.10). All carabid beetles were collected and identified in the laboratory using determination keys (Mueller 1931; Müller-Motzfeld 2006).

The hoverfly assemblage was assessed using transect counts and malaise traps (Leather 2005). Ten transects of 100 m were established in each altitudinal belt. Transect counts were conducted at the beginning of June, July and August, only on sunny days. Malaise traps were set from 15 April to 31 October in each altitudinal belt. Each trap was filled with alcohol and emptied every 13 to 16 days, 13 times. Although the traps were not replicated per altitudinal belt, it gives an indication of the phenological dynamics. The transects were positioned in areas with mixed deciduous/coniferous forest. All specimens were collected and identified in the laboratory, according to Van Veen (2004).

The passerine birds were counted at 16 points (Bibby et al. 2000). Four points were established in the low, six in the middle and six in the high altitudinal belt. Two counts were conducted: one in March/April and one in April/May. The counts were carried out during the morning hours between 5:00 a.m. and 10:00 a.m. on clear and sunny days. Every count session on the point took 5 minutes. Only forest birds which showed territorial singing behaviour were taken into account (Bibby et al. 2000).

The temperature was measured with a temperature logger (LogTag Trix–8 Temperature Recorder, accuracy \pm 0.5 °C). In each altitudinal belt, a logger was placed on the tree. The temperature was measured every six hours during the sample period.

Statistical analysis

Species assemblage, species richness and abundance per group per altitudinal belt were calculated. Data on carabid beetles and hoverflies were repeated over time and pooled for each altitudinal belt per transect for the hoverflies or trap for the carabid beetles. The relative number of animals/species per day or per 15 days was calculated for the carabid beetles and the hoverflies, respectively. In bird surveys, the maximal abundance from two counts was taken into consideration and expressed as number of territorial birds per point. A permutational MANOVA (PerMANOVA) with the Jaccard dissimilarity index was used to test the differences in species assemblages between the altitudinal belts using only the transect data (Anderson 2001). As a post hoc test, every belt was compared with the other belts using the PerMANOVA and then corrected with the Holm correction (Holm 1979). The results of the PerMANOVA were visualised with NMDS. The species replacement (Simpson similarity index) and the dissimilarity derived from nestedness in the Jaccard dissimilarity index were calculated (Baselga 2012). A rarefaction curve was prepared for every group and altitudinal belt to check whether the sampling effort was sufficient. The species-sample-based R/E curve and sample completeness curve were prepared. The differences in species richness and abundance between altitudinal belts were analysed with a Generalised Linear Model (GLM) using Poisson error distribution (McCullagh and Nelder 1989) using only the data of the transects.

The following traits were investigated: food type (hoverflies: predator, microphagous and phytophagous; birds: seeds and invertebrates), wing length and the body length of the animal. The wing length indicated the dispersal possibility as large animals with large wings having higher dispersal possibility (Delettre 1988). For the same reason, the body length was taken into account, as large animals (also non-flying animals) have a greater dispersal potential than small animals. The data on the different traits per species were extracted from the literature (Snow and Perrins 1998; Müller-Motzfeld 2006; Reemer et al. 2009; Speight 2017) or measured with the animals which were caught. The dissimilarity in traits between the different altitudinal belts was calculated with Fourth Corner Analysis using the Jaccard index (Legendre et al. 1997; Dray and Legendre 2008). For these simulations, model 1 was used, which permutates the values within each column (species) (Dray and Legendre 2008). Each group was investigated separately.

For the seasonal dynamics, the repeated data-sets of the carabid beetles and hoverflies (only malaise trap data) were used. We were only interested in the seasonal dynamics and not differences in abundance between altitudes. Therefore, the species richness and relative abundance data per period were transformed into a percentage of the total number of species/individuals per altitudinal belt.

All analyses were done with the statistics programme R (R Development Core Team 2011). For the PerMANOVA, the "adonis" function in the "vegan" package (Oksanen et al. 2013) was used. For the Fourth Corner Analysis, the "fourthcorner" function of the "ade4" package (Dray and Dufour 2007) and for the rarefaction the package "iNEXT" (Hsieh et al. 2019) were used.

Results

There was a gradual decrease in average temperature from low to the highest altitude (Table 1: $F_{2, 2855} = 63.672$, P < 0.001). All altitudes were significantly different from each other (low vs. middle: P < 0.001; middle vs. high: P < 0.001, low vs. high: P < 0.001). On average, there was a difference of approximately 3 °C between the lowest part on the north side and the top. It is interesting that the minimum temperature has a larger difference between altitude than the maximum temperature. The measured temperature between March and November in 2010 was a minimum of -4.7 °C and maximum of 32.1 °C in the lowest part and minimum -10.7 °C and maximum 31.1 °C on the top of Mt. Krim. However, these temperatures were only measured at one place on each altitudinal belt.

In total, 18 carabid species where found (Appendix 1). After rarefaction of the species diversity, it was found that almost all species were detected in carabid beetles; proportion of 0.9501 (lower altitude), 0.9927 (middle altitude) and 0.9845 (higher altitude) of detected species (Fig. 1). Carabid beetle assemblages differed across the altitudinal gradient (Fig. 2a: pseudo F = 3.08, P < 0.01). Almost 34% of the data was explained by the difference in altitude ($R^2 = 0.339$). All altitudes were significantly different from each other (low-middle: F = 3.23, P < 0.05; middle-high: F = 3.52, P < 0.05; low-high: F = 3.96, P < 0.01). Only the species turnover showed a significant difference between different altitudinal belts (Table 2). The number of species in the high altitudinal belt was not different from the other altitudinal belts (Fig. 3a: low: Z = 1.953, P = ns; middle: Z = 1.834, P = ns). However, the abundance was lower in the high altitudinal belt than the lower belts (Fig. 3b: low: Z = 4.354, P < 0.001; middle: Z = 3.160, P < 0.01). Regarding the seasonal

Table 1. Differences in temperature parameters (in °C) between altitudes in the period from March to November 2010.

Altitude	Mean	SD	Min	Max
low	13.17	6.40	-4.70	30.90
middle	11.60	6.46	-7.60	30.60
high	9.85	6.78	-10.70	31.00



Figure 1. The rarefaction of carabid beetle, hoverfly and bird species richness for different altitudes. For each species group, the species-sample-based R/E curve and sample completeness curve is shown. The triangle shows the diversity in the lower belt, the quadrant shows the diversity in the middle belt and the circle shows the diversity in the highest belt.

dynamics of the carabid beetles, it was found that the summer peak in abundance was later at higher altitudes than lower altitudes (Fig. 4a), while the summer peak in number of species was the same for all altitudes (Fig. 4b). Furthermore, there was a change in



Figure 2. NMDS plots showing the differences in assemblages between altitudinal belts for **a** carabid beetles **b** hoverflies and **c** passerine birds. The stippled line indicates the low altitudinal belt, the dashed line indicates the middle altitudinal belt and the black line indicates the high altitudinal belt.



Table 2. Beta diversity partition into species turnover and nestedness across the altitudinal gradient. The Jaccard dissimilarity index is used. Statistically significant differences marked in bold (P < 0.05).

Figure 3. Differences in **a** the number of species and **b** the abundance of beetles, hoverflies and birds across the altitudinal belts from the lowest (white bar) to the highest belt (black bar). Different letters indicate significantly different groups within one species group.

body size from lower to higher altitudes (Table 3). At the low altitude were species with larger body size (average = 19.6 mm), while in the middle altitudinal belt, carabids were smaller than those in the lower belt (16.1 mm). In the higher altitudinal belt, there were larger species on average (average 21.2 mm). All the species were carnivorous and wingless; therefore, analysis was not possible for the traits of wing length and feeding mode.

In total, 88 species of hoverflies were found, 61 species were found on the transects and 46 species with the malaise trap (Appendix 2). After rarefaction of the species di-



Figure 4. Seasonal dynamics of the number of species and abundance of carabid beetles and hoverflies at three different altitudes (485 m, 800 m and 1054 m a.s.l.). The stippled line indicates the low altitudinal belt, the dashed line indicates the middle altitudinal belt and the black line indicates the high altitudinal belt.

Table 3. Differences in the trai	ts of the assemblag	es of passerine b	oirds, carabid bo	eetles and hoverflies
between the different altitudinal	belts. * no variabilit	y in trait parame	ter within group	o species was found.

Group	Trait parameter	Stat.	Value	Р
Carabid beetles	Diet*			
	Body size	F	2.83	0.02
	Wing length*			
Hoverflies	Diet	χ^2	4.86	0.21
	Body size	F	1.19	0.25
	Wing length	F	0.67	0.47
Passerine birds	Diet	χ^2	0.29	0.65
	Body size	F	1.60	0.03
	Wing length	F	1.93	0.02

versity of the transects, it was found that almost all species were detected in hoverflies (proportion of 0.84 (lower altitude), 0.87 (middle altitude) and 0.89 (higher altitude) of detected species; Fig. 1). There were significant differences in hoverfly assemblages between the altitudinal belts (Fig. 2b: pseudo F = 2.11, P < 0.001). Only around 17%
of the data was explained by altitude ($R^2 = 0.14$). There was almost no overlap in assemblages between the high and low belt (pseudo F = 2.43, P < 0.001), but the assemblage in the middle belt largely overlapped with that in the low and the high belts, although it was still significantly different (low-middle: pseudo F = 2.24, P < 0.01; middle-high: pseudo F = 1.69, P < 0.05). Only the species turnover showed a significant difference between the different altitudinal belts (Table 2). The number of species was highest in the high altitudinal belt compared to the lower altitudes (Fig. 3a: low: Z = -2.839, P < 0.01; middle: Z = -3.361, P < 0.001). Additionally, the abundance was highest in the high altitudinal belt compared to the lower belts (Fig. 3b: low: Z = -6.821, P <0.001; middle: Z = -7.003, P < 0.001). There was a difference between the altitudinal belts in the number of species and the abundance (species: $X^2 = 10.582$, P < 0.001; abundance: X^2 = 13.558, P < 0.001). In both cases, there was a difference between the low altitudinal belt and the other two belts and no difference between the middle and high altitudinal belts. There were strong phenological differences in hoverflies for the different altitudinal belts (Fig. 4c, d). There were three peaks of hoverfly abundance. In the first two peaks, the peak in the low altitude belt was earlier than those in the middle and high altitudinal belts (Fig. 4c). The last abundance peak was in the same period in all altitudinal belts. The same pattern was found for the seasonal dynamics in species numbers (Fig. 4d). Abundance was highest in July and August, while the highest number of species was found in June. There was no difference in trait composition between the different altitudinal belts for the hoverflies (Table 3).

In total, 24 passerine bird species were recorded (Appendix 3). After rarefaction of the species diversity, it was found that almost all species were detected in birds (proportion of 0.9922 (lower altitude), 0.9885 (middle altitude) and 0.9923 (higher altitude) of detected species (Fig. 1). The bird assemblage was not significantly different between the altitudinal belts (Fig. 3c: pseudo F = 1.61, P = ns). A total of 20% of the data was explained by altitude ($R^2 = 0.199$). Species turnover and nestedness were not different for the different altitudinal belts (Table 2). The species number did not differ between the altitudinal belts, but was lower in the high altitudinal belt (Fig. 4a: low-middle: Z = -1.087, P = ns; low-high: Z = -1.525, P = ns). However, the number of species decreased gradually across the altitudinal gradient (Z = -1.985, P < 0.05). There was no difference between the low and the middle belts in terms of abundance (Fig. 4b: low-middle: Z = -1.397, P = ns), but there was a difference between the low and high altitudinal belts (Fig. 4a: low-middle: Z = -2.205, P < 0.05). Abundance gradually decreased with increasing altitude (Z = -2.462, P < 0.05). There was a change in trait composition over the different belts for body size, measured as weight and wing length (Table 3), but the trait average did not show a trend with altitudinal gradient.

Discussion

Patterns in assemblage structures for different species groups varied over the altitudinal gradient of non-fragmented montane forest area. The bird assemblage did not differ

with respect to altitude, whereas both insect groups did. Furthermore, the carabid beetle assemblage differed more with increasing altitude than that of the hoverflies. The effects of altitude on species richness and abundance between the species groups were contrasting. In both birds and carabid beetles, the abundance and number of species decreased with increasing altitude, while in the hoverfly assemblage, abundance and the number of species increased. Regarding phenology, the hoverflies showed distinct delays in abundance and species number peaks for higher altitudes in spring and early summer, while in late summer, the peaks were in the same period. Only carabid abundance showed a delay at higher altitudes, whereas the species richness peak occurred at the same time for all altitudes.

Altitudinal differences in assemblages

The first question raised was whether the discovered altitudinal patterns are caused by factors other than temperature (McCain 2009). The patterns were not due to the area (Rahbek 1997) and sampling effect (Colwell and Coddington 1994) because the study design was standardised in sampling efforts. Static evolutionary models predict that, at lower altitudes, there is more migration, which also results in higher diversity, while at higher altitudes, there is less dispersion and, thus, a higher extinction rate and lower diversity (Lomolino 2001). Due to the geographical and landscape characteristics of our study area, we were able to rule out several parameters that could contribute to the differentiation of the studied assemblages. First, the area is part of a large continuous non-fragmented forest area in the Northern Dinaric Alps in southern Slovenia, which extends further south to Croatia, so dispersion of forest species is not limited by habitat fragmentation and the extinction risk is therefore low. Secondly, the species found in the assemblages are not isolated relict populations and are distributed widely in the Dinaric Alps and beyond. Thirdly, due to the relatively short distances between sampling sites in the different altitudinal belts (< 3 km), all sites experienced similar weather conditions, especially with respect to precipitation. The patterns are in accordance with the gradient proposed by McCain (2009) and, therefore, it can be assumed that the gradient found here is driven mainly by altitudinal temperature differences.

The contrasting seasonal activity, richness and assemblage patterns observed during this study could be due to the different traits of the investigated species groups. First, the strong difference between the birds and the insect groups could be explained by differences in thermoregulation (Miller and Harley 2009). Insects are ectotherms and are dependent on the environmental temperature for development (Bale et al. 2002). In the case of the carabid beetles, there was a decrease in the number of species and abundance across a temperature gradient. In addition, insects are strongly partitioned in niches on the basis of temperature (Boggs and Inouye 2012). This means that some species are adapted to colder, higher elevation areas and some to warmer, lower elevation areas (Žagar et al. 2018). This is reflected in the strong species turnover observed in both carabid beetles and hoverflies. Birds, on the other hand, did not show any dif-

ferences in species assemblages between the different altitudinal belts. Endotherms are better adapted to different climates and only exhibit a turnover on a larger scale (Buckley and Jetz 2008). In addition, birds are extremely mobile species and almost half of the recorded species are migratory or at least partly migratory and do not overwinter at their breeding sites. The observed decrease in abundance can only be an indirect effect of temperature. Lepidoptera larvae are an important food source for the observed passerine species (Barbaro and Battisti 2011). As lepidopteran larvae are influenced by temperature, food availability might be lower at higher altitudes, which in turn affects abundances (Randall 1982; Bears et al. 2009), although this is not the case for some other insect groups (de Groot and Kogoj 2015, this study).

The dispersal ability or mobility of a species is another aspect which could result in differences in species assemblages (Hubbell 2001). This could explain the difference in assemblage patterns between the studied insect groups (the brachypterous carabid beetles and macropterous hoverflies). The non-flying carabids had a distinct assemblage for each altitude. Forest carabid beetles in our study were all brachypterous and therefore they disperse on the ground within smaller distances and have consequently smaller ranges (Kotze and O'Hara 2003; Jopp and Reuter 2005; Pizzolotto et al. 2016). Hoverflies, on the other hand, exhibited an overlap in altitudinal ranges, with the assemblages of the low and the high altitudes overlapping slightly and the assemblages of the mid altitudinal belt overlapping to a large extent with those of both the low and the high altitudinal belts. Hoverflies can fly several kilometres and some species are even migratory (Rotheray and Gilbert 2011). Therefore, they can spread over large areas relatively faster than flightless carabids. Given this, we suggest that altitude has a greater effect on the turnover of less mobile than mobile species.

On the other hand, the abundance and species richness of the hoverflies increased with altitude in forested areas. One of the reasons could be that there is competition with hymenopteran species for food resources. It was observed that, towards the north, a higher percentage of plants are pollinated by flies, because bees have their optimum at higher temperatures (Rotheray and Gilbert 2011). The abundance of Diptera species (e.g. *Cheilosia fasciata*), was found to be even negatively correlated with temperature (de Groot and Kogoj 2015), which might also be the case in other syrphid or other dipteran species (Miličić et al. 2018). Competitive relationship between hymenopteran and dipteran pollinators and even predators should, however, be explored more.

Altitudinal differences in phenology

As predicted, the carabid beetles and hoverflies exhibited different patterns of activity over the season. The phenology of hoverflies was strongly correlated with the weather. The earlier flying species showed a delay in flying with increasing altitude, which was also observed with butterflies (Illán et al. 2012). Flying in hoverflies takes a large amount of energy and mainly occurs on sunny days, when they fly in large numbers (Gilbert 1984; Gilbert 1985). The altitudinal difference in temperature was much higher in spring than in summer. This would, therefore, also influence the abundance and the species richness more strongly for hoverflies. The flightless carabid beetles showed a more stable pattern, where there was no altitudinal difference in species richness, while activity was dependent on the temperature. Additionally, carabid beetles showed a higher species turnover towards higher altitudes, which means a higher proportion of high elevation and cold adapted specialists in the carabid assemblage compared to the hoverfly assemblage. This could contribute to greater differences in phenological response across altitude in the more generalist hoverflies than in the more specialised carabids.

Altitude and climate change

Altitudinal patterns can be used to predict future patterns in a continuous habitat under the influence of climate change (Botes et al. 2006; Korner 2007; Illán et al. 2012). We found that endotherms and more mobile species had a smaller turnover than ectotherms and less mobile species, from which we can predict that the former species will undergo a less extreme shift than the latter. This was indeed found in birds, which showed no shift (Chen et al. 2011), but in butterflies, there was a strong shift, which could amount to a maximum of 100 m in 50 years (Konvicka et al. 2003; Wilson et al. 2007) or a median speed of 11 m per year (Chen et al. 2011) and for hoverflies, there was a shift predicted for several species (Miličić et al. 2018). On a latitudinal gradient, it was found that many species' ranges move northwards (Parmesan et al. 1999); however, birds have a smaller climate debt than butterflies (Devictor et al. 2012). Across a latitudinal range, the connectivity between habitats plays a very important role in species' response to climate change (Settele et al. 2008). In connected and non-fragmented natural habitats, such as temperate forests with a small altitudinal range, temperature affected insects more than birds. Therefore, it is expected that, over small ranges, birds will be less affected by climate change than insects, such as hoverflies and carabid beetles.

The results of study were constrained in time and space, as the sampling only occurred for one year and only on one mountain. As pointed out, the dynamics of the species groups can be heavily affected by the temperature and this could give different results for the different years. However, because the different belts were relatively close to each other, large annual differences would be equally impacting all the different altitudinal belts. In addition, the different belts of Mt. Krim were sampled with more transects, point counts or traps. However, this case study confirmed expected temperature driven mechanisms in assemblage changes. It is therefore important to note for future studies that additional mountains should be sampled in the same way for more years.

When examining altitudinal shifts in patterns, it is important to consider that climate change will affect different functional groups with different traits in different ways. Species that are expected to be most affected by climate change, such as ectotherms and species with poor dispersal ability, should be prioritised, as they are the best indicators for monitoring and conservation management purposes. Current monitoring and conservation programmes are mainly focused on large and charismatic species (e.g. large mammals and birds), which are usually at the top of the food chain in the ecosystem (Pereira and David Cooper 2006), but are, at least with respect to climate change, less affected and, consequently, less threatened and might not be appropriate indicators for climate-driven ecosystem changes.

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Appendix I

Altitudinal belt		Low			Middle			High	
Species	Average	Min	Max	Average	Min	Max	Average	Min	Max
Abax carinatus	0.2	0	1	0	0	0	0	0	0
Abax ovalis	1.8	1	2	0.2	0	1	0	0	0
Abax parallelepipedus	0.4	0	1	0.2	0	1	0.6	0	1
Abax parallelus	0.6	0	2	0.8	0	2	0	0	0
Aptinus bombarda	3.4	3	4	1.8	1	2	1.6	0	2
Carabus caelatus	0.2	0	1	0	0	0	0	0	0
Carabus catenulatus	1.6	0	3	0	0	0	0.4	0	1
Carabus coriaceus	1	0	3	0.6	0	1	0.4	0	2
Carabus creutzeri	0	0	0	0	0	0	0.2	0	1
Cychrus attenuatus	0.6	0	2	0	0	0	0	0	0
Licinus hoffmannseggi	0	0	0	0.2	0	1	0	0	0
Molops ovipennis	0.2	0	1	0.4	0	1	0	0	0
Molops piceus	0.6	0	1	0.6	0	1	0	0	0
Molops striolatus	0.4	0	1	1.2	0	4	0.2	0	1
Nebria dahli	0	0	0	1.2	0	2	0.4	0	1
Pterostichus burmeisteri	0	0	0	2.4	0	4	1	0	2
Pterostichus transversalis	0.4	0	1	0	0	0	0	0	0
Trechus sp.	0	0	0	0.2	0	1	0	0	0

Carabid beetle (Carabidae) species which were found per altitudinal belt. The number of individuals per 5 trap nights per altitudinal belt is shown.

Appendix 2

Average, minimum and maximum of hoverfly (Syrphidae) species abundance which were found per altitudinal belt for the transects and malaise traps.

Method		Transect							Trap			
Altitudinal Belt		Low		M	liddle		1	ligh		Low	Middle	High
Species	Average	Min	Max	Average	Min	Max	Average	Min	Max			
Baccha elongata	0.2	0	1	0.1	0	1	0.3	0	1	1	1	0
Brachypalpoides lentus	0	0	0	0.1	0	1	0	0	0	1	0	0
Brachypalpus laphriformis	0	0	0	0	0	0	0	0	0	1	1	0
Caliprobola speciosa	0	0	0	0	0	0	0	0	0	3	0	0
Callicera aenea	0	0	0	0	0	0	0	0	0	0	0	1
Chamaesyrphus scaevoides	0	0	0	0	0	0	0.1	0	1	0	0	0
Cheilosia antiqua	0	0	0	0.1	0	1	0	0	0	0	0	0
Cheilosia chloris	0	0	0	0	0	0	0	0	0	0	1	0
Cheilosia himantopa	0	0	0	0.1	0	1	0.1	0	1	0	0	0
Cheilosia impressa	0	0	0	0.1	0	1	0	0	0	0	0	0
Cheilosia lasiopa	0.1	0	1	0	0	0	0.1	0	1	0	0	0
Cheilosia melanopa	0	0	0	0	0	0	0.1	0	1	0	0	0
Cheilosia pagana	0.1	0	1	0	0	0	0.1	0	1	0	0	0
Cheilosia personata	0	0	0	0	0	0	0	0	0	0	0	1
Cheilosia scutellata	0.1	0	1	0	0	0	0.1	0	1	0	0	0
Cheilosia vulpina	0.2	0	1	0	0	0	0.3	0	1	0	0	0
Chrysostoxum lessonae	0	0	0	0	0	0	0	0	0	1	0	0
Chrysotoxum arcuatum	0	0	0	0	0	0	0	0	0	0	4	3
Chrysotoxum bicinctum	0	0	0	0	0	0	0	0	0	0	0	12
Chrysotoxum elegans	0	0	0	0	0	0	0	0	0	0	0	1
Chrysotoxum fasciolatum	0	0	0	0	0	0	0	0	0	1	0	7
Chrysotoxum festivum	0	0	0	0	0	0	0.1	0	1	2	1	0
Chrysotoxum intermedium	0.1	0	1	0	0	0	0	0	0	6	13	4
Chrysotoxum octomaculatum	0	0	0	0	0	0	0	0	0	0	11	6
Chrysotoxum vernale	0	0	0	0	0	0	0.1	0	1	1	1	0

Method Transect										Trap		
Altitudinal Belt	Low			Middle				ligh		Low	Middle	High
Species	Average	Min	Max	Average	Min	Max	Average	Min	Max			
Chrystoxum arcuatum	0	0	0	0	0	0	0	0	0	0	0	1
Criorhina berberina	0	0	0	0	0	0	0	0	0	2	4	1
Criorhina floccosa	0	0	0	0	0	0	0	0	0	0	1	0
Dasysyrphus albostriatus	0	0	0	0	0	0	0.1	0	1	0	0	0
Dasysyrphus friuliensis	0	0	0	0	0	0	0	0	0	0	0	1
Dasysyrphus venustus	0	0	0	0	0	0	0.1	0	1	0	1	1
Didea fasciata	0	0	0	0	0	0	0	0	0	0	1	0
Epistrophe eligans	0.1	0	1	0	0	0	0	0	0	0	0	0
Epistrophe flava	0	0	0	0.1	0	1	0	0	0	0	0	0
Epistrophe grossulariae	0.1	0	1	0.1	0	1	0.2	0	1	0	0	0
Episyrphus balteatus	1	1	1	0./	0	1	0.9	0	1	8	39	35
Eristalis interrupta	0	0	0	0	0	0	0.1	0	1	0	0	0
Eristalis pertinax	0	0	0	0	0	1	0.2	0	1	0	0	0
Eristalis similis	0	0	1	0.2	0	1	0.0	0	1	0	0	0
Eristalis tenax	0.1	0	1	0.2	0	1	0.2	0	1	0	0	0
Eumerus amoenus	0.1	0	1	0	0	0	0	0	0	0	2	0
Eumerus juviursis	0	0	0	0 /	0	1	02	0	1	0	1	4
Eupeoues imponitus	0	0	0	0.4	0	1	0.2	0	1	1	1	4
Eupeoaes luniger Molangung gingta	0	0	0	0	0	0	0	0	0	1	2	1
Melangyna cincia Melangyna i sonot ositanum	0	0	0	0	0	0	0 1	0	1	0	2	1
Melangyna compositarum	0	0	0	0	0	0	0.1	0	1	0	1	1
Molangyna iasiophthaima	0	0	0	0	0	0	0	0	0	0	1	1
Melangyna umbellalarum	0	0	0	0	0	0	0 1	0	1	2	0	5
Melimanosioma scatare	0	0	0	0	0	0	0.1	0	1	1	1	4
Meligramma cingulata Melioogong gunicollic	0 1	0	1	0	0	0	0	0	0	2	1	1
Meliscaeva airectalla	0.1	0	1	0 1	0	1	0 0	0	1	11	17	26
Menscaeva cinciena Maradan cinarauc	0.4	0	0	0.1	0	1	0.8	0	0	0	1/	0
Manadam annatam	0	0	0	0.1	0	1	0	0	0	0	0	0
Merodon equestris	0	0	0	0.2	0	0	0	0	0	0	0	1
Meradan equestris	0	0	0	0.4	0	1	0.1	0	1	0	0	0
Microdon devins	0.1	0	1	0.4	0	0	0.1	0	0	0	0	0
Myathropa florea	0.1	0	0	0	0	0	0	0	0	1	0	2
Myathropa florea	0.6	Ő	1	0 1	õ	1	03	õ	1	0	Ő	0
Paragus albifrons	0.1	õ	1	0	õ	0	0	õ	0	Ő	Ő	Ő
Paragus haemorrhous	0.2	0	1	0	0	0	0	0	0	0	0	õ
Paragus pechiolli	0.1	0	1	0	0	0	0	0	0	0	0	õ
Parasyrphus lineolus	0	0	0	0	0	0	0.1	0	1	0	0	õ
Parasyrphus macularis	0	0	õ	0	0	0	0.1	0	1	0	1	1
Parasyrphus malinellus	0.1	0	1	0	0	0	0	0	0	0	0	0
Parasyrphus punctulatus	0	0	0	0	0	0	0	0	0	1	0	1
Pipiza bimaculata	0	0	0	0.1	0	1	0	0	0	0	0	0
Pipiza quadrimaculata	0	0	0	0	0	0	0.2	0	1	0	0	0
Pipizella bispina	0	0	0	0.3	0	1	0	0	0	0	0	0
Platycheirus albimanus	0.1	0	1	0.3	0	1	0.1	0	1	0	0	4
Platycheirus cf. scutatus	0	0	0	0	0	0	0.3	0	1	0	1	1
Scaeva pyrastri	0	0	0	0	0	0	0.1	0	1	0	0	0
Sphaerophoria sp.	0.1	0	1	0	0	0	0	0	0	0	0	0
Sphegina clunipes	0.2	0	1	0	0	0	0	0	0	0	0	0
Sphegina sibirica	0	0	0	0	0	0	0.3	0	1	0	0	0
Sphegina verecunda	0.1	0	1	0	0	0	0	0	0	0	0	0
Syritta pipiens	0	0	0	0	0	0	0.1	0	1	0	0	0
Syrphus ribesii	0.2	0	1	0.6	0	1	0.9	0	1	0	2	9
Syrphus torvus	0	0	0	0.2	0	1	0.1	0	1	0	1	1
Syrphus vitripennis	0.1	0	1	0.3	0	1	0.6	0	1	0	1	4
Temnostoma vespiforme	0.4	0	1	0.2	0	1	0	0	0	0	0	0
Volucella inanis	0	0	0	0.1	0	1	0	0	0	0	0	0
Volucella pellucens	0.5	0	1	0.2	0	1	0.3	0	1	0	1	0
Xanthogramma laetum	0	0	0	0	0	0	0	0	0	1	2	1
Xanthogramma pedissequum	0	0	0	0	0	0	0	0	0	0	1	0
Xylota segnis	0.2	0	1	0.1	0	1	0.1	0	1	0	0	0
Xylota sylvarum	0	0	0	0	0	0	0	0	0	0	1	1

Appendix 3

Passerine bird species (Aves, Passeriformes) per altitudinal belt. The average number, minimum and maximum of individuals per count point per altitudinal belt is shown.

Altitudinal belt		Low			Middle			High	
Species	Average	Min	Max	Average	Min	Max	Average	Min	Max
Anthus trivialis	0.25	0	1	0.00	0	0	0.50	0	1
Certhia familiaris	0.00	0	0	0.17	0	1	0.50	0	2
Chloris chloris	0.25	0	1	0.00	0	0	0.00	0	0
Coccothraustes coccothraustes	0.25	0	1	0.00	0	0	0.00	0	0
Erithacus rubecula	4.00	3	5	3.67	3	5	3.17	2	4
Fringilla coelebs	4.00	3	6	4.67	3	6	4.00	2	5
Garrulus glandarius	1.25	0	2	0.33	0	2	0.83	0	2
Lophophanes cristatus	0.50	0	1	0.50	0	2	0.17	0	1
Loxia curvirostra	0.00	0	0	0.00	0	0	0.17	0	1
Nucifraga caryocatactes	0.00	0	0	0.00	0	0	0.17	0	1
Oriolus oriolus	0.25	0	1	0.00	0	0	0.00	0	0
Parus major	1.75	1	3	0.67	0	2	0.33	0	1
Periparus ater	2.50	2	3	2.67	1	4	2.83	0	5
Phylloscopus collybita	1.50	1	2	0.83	0	2	1.17	1	2
Poecile palustris	0.75	0	1	0.33	0	1	0.50	0	1
Pyrrhula pyrrhula	0.00	0	0	0.33	0	2	0.00	0	0
Regulus ignicapilla	0.75	0	2	0.50	0	2	0.50	0	2
Regulus regulus	0.50	0	2	0.33	0	1	0.67	0	2
Sitta europaea	0.75	0	3	0.00	0	0	0.00	0	0
Sylvia atricapilla	2.00	1	3	2.50	2	3	2.17	1	4
Troglodytes troglodytes	0.50	0	1	1.00	0	2	0.00	0	0
Turdus merula	2.00	2	2	0.67	0	1	1.50	1	2
Turdus philomelos	0.75	0	1	1.50	1	2	1.33	1	2
Turdus viscivorus	0.25	0	1	0.33	0	1	0.33	0	1

SHORT COMMUNICATION



Wild mammal dung abundance in Lake Mburo National Park is lower than in adjacent ranchlands

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Abstract

The establishment of livestock ranchlands adjacent to protected areas in savanna ecosystems is believed to threaten wild animals. Intensive competition for vegetative resources, water and poaching are considered to be immediate factors that reduce the capacity of protected areas to sustain wild mammals. The coexistence of wild mammals and ranchlands is common in Southern Africa but has rarely been suggested as a viable conservation option in East Africa. To assess the importance of ranchlands in conserving wild mammals, 36 plots of 20×20 m dimension were positioned along a 7240 m stretch from the boundary in Lake Mburo National Park (LMNP) and 36 plots of similar dimension were set within the ranchlands adjacent to the Park. The dung counts of different species recorded in the plots were used as a relative index of mammal abundance in the ranchlands and in LMNP. The results reveal 18 wild mammal species recorded in both sampled areas, 12 within LMNP and 17 in the adjacent ranchlands. The topi Damaliscus lunatus was only found in the park. Total dung count estimated in both ranchlands and LMNP was 2,586 with LMNP accounting for 29% and ranchlands 71%. In terms of wild mammal dung, ranchlands had a higher wild mammal dung count than LMNP (30% higher). The study points to the compatibility of the two land uses in conserving wild mammals and biodiversity in general, negating the common belief of competition and exclusion. Future research is needed on the compatibility of ranchlands with protected areas on biodiversity status of other species.

Keywords

abundance, cattle, land use, livestock, protected area, ranches, savanna, Uganda, wild mammals

Introduction

The assumption that biodiversity is higher in protected areas than in other land uses has dominated biodiversity conservation discourse (Stoner et al. 2007; Geldmann et al. 2013; UNEP-WCMC et al. 2018). This assumption is further supported by the fact that land use is among the major threats to biodiversity (Sala et al. 2000; Asner et al. 2010). To conservation purists, the exclusion of land uses that are perceived to be incompatible with protected areas is the best way to counter biodiversity loss. Unfortunately, exclusion has not completely halted the loss of biodiversity in protected areas and in some cases has exacerbated human-wildlife conflict since communities still want to access essential resources within the protected areas (Mistry and Beradi 2000; Lindsey et al. 2012). The demand for land and its resources in areas adjacent to protected areas managed for biodiversity conservation is increasingly putting pressure on biodiversity conservation areas, prompting the need for land use options that can simultaneously conserve biodiversity and serve other production uses (Prins 1992; Marchant 2010). Such land uses act as dispersal areas for wild animals especially where the land tenure system does not restrict access to environmental resources (Okello and Kioko 2010).

Lake Mburo National Park (LMNP), the smallest grassland protected area (260 km²) in Uganda located within a dryland savanna, is surrounded by livestock ranchlands (Blösch 2002). The land tenure systems in Lake Mburo include private property, non-property, customary communal and customary individualized tenure (Kisamba-Mugerwa et al. 2006). The creation of the park resulted in local resistance and ensuing socio-political conflicts (Marquardt et al. 1994). Grazing land was reduced and livestock restricted from entering the gazetted park area since grazing was perceived to be incompatible with wildlife conservation. However, the decision to exclude livestock grazing from the park was not guided by any critical study to assess whether exclusion was the best option for conserving biodiversity. Using dung counts of wild mammals in LMNP and the adjacent ranchlands, this study assesses the compatibility of the two intensive land uses in conserving wild mammals. The aim of this study is to test the common assumption that biodiversity is higher in protected areas than on other land uses.

Methods

The study was conducted in the eastern part of LNMP and the adjacent ranchlands, in Kiruhura District, South Western Uganda. The park lies at an altitude of about 1200 m above sea level, average annual rainfall of 888 mm and mean annual temperatures of 22.9 °C are recorded at the nearest weather station in Mbarara (Blösch 2002). The park is part of the Kagera savanna ecosystem (Blösch 2002). The original vegetation is classified as dry *Vachellia* Savanna with *Vachellia* species being dominant (Langdale-Brown et al. 1964) though currently savanna vegetation is heavily degraded leaving a woody layer of *Acacia hockii* (Blösch 2002). Mammalian wildlife currently inhabiting the park

include zebra *Equus quagga boehmi*, impala *Aepyceros melampus*, waterbuck *Kobus ellipsiprymnus*, eland *Taurotragus oryx*, topi *Damaliscus lunatus*, warthog *Phacochoerus africanus* and bushbuck *Tragelaphus scriptus*. The Ankole cattle *Bos taurus* and goats *Capra hircus* are the common livestock (Blösch 2002; Rannestad et al. 2006). LMNP is largely used for wildlife conservation and recreation/ tourism. Outside the park, ranchland and communal grazing lands are the major land use types (Kagoro-Rugunda 2004; Rannestad et al. 2006).

I systematically paired sites in LMNP and the adjacent ranchlands running parallel to the boundary across the two land uses between June and September 2015. The boundary between LMNP and the ranchlands is unfenced and demarcated with concrete pillars. The herbaceous vegetation on either side of the boundary is different but the woody vegetation is similar (Nyamukuru et al. 2019). Additionally, the herbaceous composition is associated with mammals and the grazing intensity is different between the ranchlands and LMNP (Nyamukuru et al. 2019; Nyamukuru et al. unpublished data). In total, four sites of 1060 m each in LMNP and in the ranchlands were paired (Figure 1). In each site, I established 9 plots of 20×20 m, giving a total of 72 plots. The plots were positioned at progressive distances of 300, 420 and 540 m away from the boundary into LMNP and the same distances were applied from the borders into the ranchlands. The distance of 300 m away from the boundary was applied to avoid the edge effect (Broadbent et al. 2008). Furthermore, wild animals maintain a shorter distance away from grazing (livestock) than from other human activities like agriculture and settlement (Okello and Kioko 2010). I recorded mammals by looking at the presence and frequency of dung piles in 20×20 m plot. The chances of finding dung piles were equally likely on both sides of the boundary. The dung pile was identified and attached to mammal species with the help of an experienced game ranger. The dung counts in this study are used as a proxy for biodiversity, distribution and relative abundance of mammals. The assumption is that if dung count rates are higher in the ranchlands than the national park, this may suggest that the population density could be higher in the ranchlands that produce it. The dung counts were used over alternative methodologies because studies have shown that they are accurate estimates of mammal population biomass and density (Barnes 2001; Young et al. 2005; Boafo et al. 2009). Secondly, the dung method was used in this study because I assumed that a short distance of 540 m away from the boundary will capture animals with both large home range and those that range near the boundary. Although the distance seems small, from the data, that error does not affect the results and the conclusion. The use of dung to estimate mammal densities and biomass has also been demonstrated by several researchers (Karanth and Sunquist 1992; Plumptre and Harris 1995; Young et al. 2005). To test whether the relative abundance of wild mammals is greater inside LMNP than the adjacent ranchlands, a generalized linear mixed effect model with a restricted maximum likelihood (nlme R package) was used. The dung count in the model was used as a response variable and land use as a predictor variable. Random factors were mammal species identity and plot. The distance from the boundary was added to the model after testing the effect of land use to test if it could explain additional differences. The analysis was performed using R statistical software (R Development Core Team 2016).



Figure 1. The sampling design within Lake Mburo National Park and ranchlands. Eight sites (4 in LMNP and 4 in ranchlands) were sampled out; in each site 9 plots of 20 × 20 m were designated.

Results and discussion

Results from the study reveal the presence and distribution of wild mammals within the two land uses. In total, 18 wild mammals were found to range within the sampled corridor, with ranchlands recording more (17) wild mammal species than LMNP (Table 1). There is a significant difference in dung counts between LMNP and the ranchlands

(estimate =0.55, standard error = 0.17, z value = 3.21, p < 0.01). Ranchlands still held a higher wild mammal dung count (1,183) as compared to LMNP (629) suggesting that the population density could be higher in the ranchlands, and that they are a preferred site for wild mammals. The distance from the boundary did not explain any additional variations (estimate = -0.00, standard error <0.01, z value = -1.61, p = 0.11) implying that land use or a different factor influences the relative abundance of wild mammals. The likely factor is the variation of the herbaceous vegetation in the two land uses (Nyamukuru et al. 2019) which could suggest different diet in the ranchlands and LMNP. Studies further reveal the presence of cattle *Bos taurus* and horses *Equus caballus* within LMNP but no goats *Capra hircus* (Table 1). The distribution of individual species within the two land uses based on study results shows a coexistence of livestock and wild mammals. Zebra *Equus quagga boehmi*, cattle *Bos taurus* and eland *Taurotragus oryx* had a higher dung count in the ranchlands than LMNP, bushbuck *Tragelaphus scriptus*, bush duiker *Sylvicapra grimmia*, dwarf mongoose *Helogale parvula* and goat *Capra hircus* were only found in the ranchlands (Table 1).

Results of the survey indicate that contrary to received conventional wisdom (Geldmann et al. 2013) ranchlands returned a higher relative abundance of wild mammals than LMNP. This is evidence that wild mammals either periodically migrate from

English name	Zoological name	Lake Mburo National Park	Ranchlands
-	-	Dung cour	its
Wild mammals		-	
Zebra	Equus quagga boehmi	266	538
Buffalo	Syncerus caffer	163	6
Warthog	Phacochoerus africanus	68	28
Impala	Aepyceros melampus	66	466
Eland	Taurotragus oryx	31	82
Baboon	Papio anubis	12	9
Торі	Damaliscus lunatus	8	_
Waterbuck	Kobus ellipsiprymnus	6	10
Hippopotamus	Hippopotamus amphibius	5	3
Bush pig	Potamochoerus larvatus	2	2
African hare	Lepus victoriae	1	7
Bushbuck	Tragelaphus scriptus	_	3
Bush duiker	Sylvicapra grimmia	_	12
Monkey	Cercopithecus aethiops	1	3
Hare	<i>Lepus</i> spp	_	6
Mongoose	Helogale spp.	_	4
Dwarf mongoose	Helogale parvula	_	2
Hyaena	Crocuta crocuta	_	2
Total		629	1,183
Livestock			
Ankole cattle	Bos taurus	122	619
Horse	Equus caballus	1	23
Goat	Capra hircus	_	9
Total		123	651

Table	1.7	The dun	g counts	of wild	mammals	and	livestock	recorded	in	Lake	Mburo	National	Park	and
the adj	jacen	t ranchl	ands.											

the Park to neighboring land uses or live there as residents as also observed by Guard (1991) and Averbeck (2002) in Lake Mburo ecosystem. The presence of bushbuck *Tragelaphus scriptus*, hyaena *Crocuta crocuta*, mongoose *Helogale* spp., hare *Lepus* species and bush duiker *Sylvicapra grimmia* on ranchlands and not LMNP further demonstrates the lack of imminent threats to these animals on the ranchlands but rather a possibility of coexistence. By choosing to range on ranchlands rather than the protected area, these species affirm the existence of more suitable ecological conditions and the differences in habitat selection by different species. A similar study by Okello and Kioko 2010 found that the likelihood of finding several species in Olgulului – Ololorashi Group Ranch was high compared to Amboseli National Park due to the different ecological needs of species. The existence of cattle *Bos taurus* in the park, and not goats *Capra hircus*, also points to greater and deeper functional relationships between specific species and rangelands. These results are also supported by Rannestad et al. (2006) who undertook similar studies in Lake Mburo using a different approach of line transect distance sampling method in the same study sites but at a wider scale.

The coexistence of wild mammals and livestock in rangelands as demonstrated by studies conducted in such lands (Jensen 2001; Niamir-Fuller et al. 2012), has tended to overshadow the conflict narrative. Local communities have, amidst challenges, sustained their different livelihoods in such environments. The Lake Mburo scenario is an example; before gazetting and demarcating the park in 1983, pastoralists coexisted with wildlife for a long time dating back to the 1800s when the ecosystem was a traditional grazing land and hunting ground for the King (Marquardt et al. 1994). However, against that, Caro et al. (1998) and Crosmary et al. (2015) reported higher wild mammal densities in the protected area than the adjacent land uses. Furthermore, the presence of wild mammals in ranchlands means that these land uses are dispersal areas of LMNP and hence relieving the wild mammal population density pressure from the small park.

Conclusions

Notwithstanding studies that suggest greater competition and conflict between wildlife and other land uses (Prins 2000; Young et al. 2005; Niamir-Fuller et al. 2012), results from this study tend to demonstrate the positive conservation value of ranchlands in the conservation of biodiversity, specifically wild mammals. However, given the delicate nature of wildlife-human interface, there is need for further research on the biodiversity status of other species in the ecosystem to reach a conclusive and informed decision on the compatibility of the two land use types within the greater Lake Mburo ecosystem and its conservation goals. Given the existence of wild mammals in ranchlands and livestock in LMNP as demonstrated in this study, it is important that LMNP and nearby land owners reach agreed management positions. The two parties ought to come up with strategic action on resolving compensation and injury claims raised by ranchers as well as livestock that stray into the LMNP.

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CONSERVATION IN PRACTICE



Large carnivores and zoos as catalysts for engaging the public in the protection of biodiversity

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Abstract

Addressing the biodiversity crisis requires renewed collaborative approaches. Large carnivores are ambassador species, and as such they can aid the protection of a wide range of species, including evolutionarily distinct and threatened ones, while being popular for conservation marketing. However, conflicts between carnivores and people present a considerable challenge to biodiversity conservation. Our cross disciplinary essay brings together original research to discuss key issues in the conservation of large carnivores as keystone species for biodiversity rich, healthy ecosystems. Our findings suggest the need to promote coexistence through challenging 'wilderness' myths; to consider coexistence/conflict as a continuum; to include varied interest groups in decision making; to address fear through positive mediated experiences, and to explore further partnerships with zoos. As wide-reaching institutions visited by over 700 million people/ year worldwide, zoos combine knowledge, emotion and social context creating ideal conditions for the development of care towards nature, pro-environmental behaviors and long-term connections between visitors and carnivores. Based on current research, we provide evidence that large carnivores and zoos are both powerful catalysts for public engagement with biodiversity conservation, recognizing barriers and suggesting future ways to collaborate to address biodiversity loss.

Keywords

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conservation biology; human-wildlife conflict; large carnivores; ambassador species; zoos; biodiversity conservation

Introduction

Awareness of biodiversity values and sustainable use are key concerns in mainstreaming biodiversity across society and halting its loss (Aichi Target 1 https://www.cbd.int/ sp/targets/rationale/target-1/default.shtml). Research indicates that biodiversity is not salient to people (Consorte-McCrea et al. 2017a; Legagneux et al. 2018) yet evidence shows that developing strong connections with charismatic species, large carnivores (e.g. bears, big cats, wolves, elephant seals) in particular, could benefit biodiversity conservation as large carnivores are "ambassador species" – species whose range overlap greatly with that of EDGE – Evolutionarily Distinct and Globally Endangered – species, while being popular amongst the public (Macdonald et al. 2017). Nevertheless, conflict and fear may pervade the relationship between people and carnivores, especially in rural areas.

Research also indicates that social context and experience together with proenvironmental messaging can promote the development of a connection with nature and pro-environmental behaviors (Clayton et al. 2017a), reduce fear and address conflict. Such conditions are often provided by zoos, where large carnivores are a familiar feature.

This paper offers a synthesis of contributions presented at the symposium "Large carnivores and zoos as catalysts for biodiversity conservation: how do we engage the public in the protection of biodiversity?" at the European Congress for Conservation Biology (ECCB), Finland 2018. Bringing together natural and social sciences, as well as psychology and education, it provides a rich multifaceted approach to the conservation of biodiversity by exploring the connections between people, large carnivores and zoos. We review research that addresses key challenges to the acceptance of large carnivores and examine the role of zoos in promoting connection to nature, exploring solutions, and suggesting future ways in which programs for the conservation of these charismatic species and zoos can collaborate to achieve public commitment towards biodiversity conservation.

The return of a biodiversity keystone

Large carnivores are considered catalysts for the conservation of biodiversity due to their charisma, their role in regulating ecosystem dynamics and their rich cultural and historical heritage (Linnell et al. 2005; Macdonald et al. 2017). Research suggests that there are many links between wild predators and enhanced biodiversity (see Sergio et al. 2006 for a review; Lennox et al. 2018; O'Bryan et al. 2018). As humans removed large carnivores as apex predators in ecosystems worldwide, classic trophic level cascades were transformed into systems dominated by smaller carnivores and herbivores, putting pressure on plant species composition and abundance, and resulting in loss of biodiversity (McShea 2005; Steneck 2005; Lennox et al. 2018). Despite their key stone role in biodiversity, large carnivores are often not welcomed by people; their presence may cause tensions and be at the root of historic human-wildlife conflict.

Changes in land use combined with widespread bounties on large carnivores since the middle ages, culminated in their steep decline across many countries (Trouwborst 2010). However, a combination of factors beginning in the last decades of the 20th century have resulted in a transformed scenario: although the human population has never been higher, over 50% is now concentrated in urban areas (Hinds and Sparks 2008). As a result forests have regenerated, providing the necessary resources for the return of many species of herbivores, which together with protective legislation enabled the return of wild carnivores (Trouwborst 2010). Nevertheless, an increase in large carnivores' populations may affect public attitudes towards them in the future (Eriksson et al. 2015).

Interactions between people and carnivores are interpreted differently by different people. These interactions can give rise to conflicts not only between people and large carnivores, but also between social groups. The first type of conflict often reflects concerns related to fears for own safety or that of others, or fear of loss of other favored species (Knight 2001; Frank et al. 2015; Carter and Linnell 2016), but also concerns associated to material interests related to game, farming or property. The second type of conflict rather reflects socio-economic tensions between interest groups or other social groups formed by an urban-rural divide (Skogen et al. 2008). Such concerns and tensions play into people's negative attitudes towards the presence of wild carnivores and lack of support towards conservation (Bath et al. 2008; Torkar et al. 2010; Johansson et al. 2012a). High levels of knowledge about carnivores, on the other hand, have been associated with positive attitudes towards them, particularly when knowledge comes from trusted sources (Kellert et al. 1996; Roskaft et al. 2007; Glikman et al. 2012).

Due to continuous changes in land use, areas of healthy habitat and protected areas are usually small and fragmented and cannot sustain many wild carnivores. Therefore, local landowners and the general public become necessary partners in the survival of wild populations. Even more than a need for a pristine habitat, the success of conservation and recovery of carnivores, hence biodiversity, depends on the involvement of interest groups in the process, and public support (Amit and Jacobson 2018; Bombieri et al. 2018). While we need to engage people in conservation, coexistence presents new challenges. Although in areas where wild carnivores have persisted people have developed strategies to coexist with them, in areas where they have returned after a long absence such practices may have been lost and conflicts may ensue (Linnell et al. 2005; Musiani et al. 2009; Trouwborst 2010).

Taking steps towards coexistence with large carnivores

One way of promoting coexistence requires rethinking the separation between human areas and wildlife areas. Large carnivores show capabilities to adapt to different humandominated ecosystems across the world (Woodroffe et al 2005; Ahmadi et al. 2014; Blackburn et al. 2016), which supports the idea that separation is not a necessary condition for large carnivore conservation (López-Bao et al. 2017). Evidence supporting the idea of coexistence with large carnivores can be found worldwide (e.g., Zimmermann et al. 2010; Morell 2013; Chapron et al. 2014; Alexander et al. 2016). The challenge remains whether human societies can accept and adapt to non-predator-free landscapes (Carter and Linnell 2016; López-Bao et al. 2017), and how to engage the public support of such a group of contentious species.

Addressing the challenge of human-large carnivore coexistence requires multiple steps at the individual, societal and institutional levels. For example: i) removing the symbolic value of large carnivores: nowadays large carnivores are symbolically linked to wilderness and remoteness, and the notion that these elements are important for their conservation has prevailed in many contexts, shaping the range of these species (López-Bao et al. 2017); ii) promoting adaptation of human behavior to reduce risks and costs of coexisting with large carnivores (Carter and Linnell 2016): appropriate livestock husbandry practices (e.g., protecting free-ranging livestock at night, Pimenta et al. 2017) and the implementation of interventions to decrease the likelihood of carnivore attacks (van Eeden et al. 2018) may contribute to make farming activities compatible with large carnivores (Bruskotter and Wilson 2014; López-Bao et al. 2017; O'Bryan et al. 2018).

Living with large carnivores: looking at the glass half-full

It is useful to look at both negative and positive aspects of human-carnivores interactions as part of a continuum. Conflict or coexistence are not just opposite terminologies used to define human-wildlife interactions; they also represent the lenses we choose to use when addressing any interaction between people and wildlife. Conceptualizing human-wildlife interactions as wildlife threatening human interests and livelihood may limit the understanding of the deep-rooted reasons behind conflicts, which are often better defined as human-human conflicts (Young et al. 2010; Bhatia et al. 2016; Madden and McQuinn 2017). Moreover, by focusing on conflicts all the neutral to positive interactions between humans and wildlife can be overlooked, hiding the fact that often people and wildlife do coexist in a shared landscape.

To better include coexistence in human-wildlife interaction discourses, Frank (2016) introduced the conflict-to-coexistence continuum framework. This continuum addresses the entire range from negative to positive attitudes and/or behaviors toward wildlife, which encompasses the different degrees of conflict and coexistence that typify human-wildlife interactions. The type of interaction is context-laden and varies depending on an array of factors, from the costs and benefits of sharing the landscapes with wildlife to social and cultural context, including human-human interactions (Morzillo et al. 2014; Frank 2016; Yurco et al. 2017). Conflict-to-coexistence dispositions toward wildlife are dynamic and can change over time, across geographical scales, and in intensity, shifting along the continuum as interactions are not about the presence or absence of conflict or coexistence; they are about how the relationship shifts along the conflict-to-coexistence continuum over space and time and across species. The challenge is how to move the discourse toward more inclusive and positive relations with wildlife.

As the resolution of human-large carnivore conflict is often delegated to wildlife managers, the engagement of local people in decision making can be a rare occurrence. Traditional tools often fail to drive diverse interest groups to consensus and the resolution of conflicts. Methods such as the applied human dimensions facilitated workshop approach (AHDFWA) focus on building strong relationships and teams to solve current people-wildlife conflicts, achieving success in addressing challenges of living with wild carnivores across the globe (Hazzah et al. 2017; Schulz et al. 2017). According to Alistair Bath, "it is important to take the time to effectively move beyond *engagement* to a *committed relationship* of trust to achieve consensus and conservation successes."

Considering that the occurrence of predator attacks on humans is rare, tolerance of risks is affected by norms, culture, spiritual beliefs, cognitive and emotional factors, including risk perception (Carter and Linnell 2016; Bombieri et al. 2018; Struebig et al. 2018). Therefore, one of the priorities in large carnivore conservation must be to break down barriers by finding strategies to address and manage people's fears and perceptions of risk. The following sections explore these points in greater detail.

Addressing people's fear in large carnivore conservation: a case study from Sweden

Although most people in Sweden hold a positive attitude towards biodiversity conservation (Lindström et al. 2006) some may see the presence of large carnivores as a positive and rewarding experience, while others may respond with feelings of fear for themselves or their children and pets. These emotions must be taken into consideration in biodiversity conservation as they have implications for people's quality of life (Flykt et al. 2013), and are associated with attitudes towards wildlife policy and acceptance of management measures (Johansson et al. 2012a; Jacobs et al. 2014; Frank et al. 2015)

The diverse feelings evoked towards carnivores could partly be explained by people's different appraisal of what an encounter with the species would be like. Individuals who think about such an encounter as a potential danger and think they would be unable to predict the animal's behavior in the situation and consider their own reaction as uncontrollable, express stronger fear (Johansson et al. 2012a, 2012b; 2016a).

In the case of brown bears, the literature proposes four major groups of fear interventions: information and education, exposure to animal and habitat, collaboration and participation, and financial incentives (Johansson et al. 2016a). But the effects of these interventions on people's feelings of fear are rarely evaluated. From a psychological point of view the intervention would only contribute to reduced feelings of fear if an encounter with the species is re-appraised in relation to coping strategies. Two such interventions were developed in collaboration with researchers in wildlife ecology, large carnivore information centers and wildlife parks in Sweden: information meetings, and guided walks close to radio-collared brown bears (Johansson et al. 2016b, 2017). Results suggested that both interventions can decrease fear of brown bears if there is an opportunity to re-appraise the potential consequences of a brown bear encounter. This suggests that both the design of information content, and the social and environmental contexts are important. Key aspects were a) a positive social interaction with a presenter or guide with personal experience of brown bear encounters who could serve as a role model for appropriate behavior in brown bear areas, and b) the opportunity to gain an understanding of how brown bears use the terrain. Therefore, guided walks in brown bear areas may be a more efficient approach than information meetings indoors. Similar experiences could be promoted in wildlife parks and zoos (Johansson et al. 2019).

To what extent the reduced feelings of fear also influence people's attitudes towards brown bears remains to be seen, but they could strengthen a positive emotional connection with nature. In this next section we will take a closer look at the role of emotional connection and an understanding of care in the context of biodiversity.

Building a committed relationship with biodiversity through concern and care

Research points to lack of interest in nature and reduced commitment to biodiversity conservation as being linked to cognitive elements such as misconceptions and negative messages about wildlife in formative years (Velsor and Nilon 2006; Consorte-McCrea et al. 2017b) and to declining opportunities to engage with nature from childhood. This phenomenon has been described as the *extinction of experience* (Pyle 2002). While the *biophilia hypothesis* (Kellert and Wilson 1993) proposes we evolved an intrinsic emotional bond with other living organisms, there are suggestions that "learning, culture and experience" are necessary to strengthen this fragile bond (Kellert 2002; Hinds and Sparks 2008: 110).

People's progressive amnesia of what the landscapes were like before large carnivores disappeared may result in acceptance of natural spaces devoid of carnivore species (see Kahn and Kellert 2002; Steneck 2005). However, beyond their role in ecosystem dynamics, wild carnivores can help us connect with nature, "put some of the wild back into our lives", and help us glimpse into the dynamics and interconnections that are at the essence of biodiversity (Linnell et al. 2005: 399; Boitani and Linnell 2015). In-

terestingly, research suggests that affective experiences provide important entry points for connection with large carnivores (Millar and Millar 1996; Kellert 2002; Roskaft et al. 2007). In rural Norway, positive attitudes towards wolves were associated with expectations of seeing them in the wild (and with the excitement derived from these encounters) (Roskaft et al. 2007).

Connection with nature can also relate to a sense of responsibility and stewardship towards it and concerns for future generations (Novacek 2008). Findings from focus groups carried out in the UK are in line with this argument (Consorte-McCrea et al. 2017a). Participants held strong views about collective responsibility:

"I think for people with children, they've got to look at the future of their children as living as part of the planet. That if we introduce these [carnivores], it will benefit their children because there will be more forests and natural environments for our animals and show that as a positive thing for the adults of children [sic], that's what they're going to grow up with. It's not going to be a major threat to your child, it's going to be a positive step for them in the future."

A moral purpose is necessary to motivate society to meet challenges such as the ones presented by biodiversity loss, shifting the focus from individual moral choices to "our collective ability to recognize, reflect upon, and reasonably address the value questions we face." (Clayton and Myers 2009: 53). The contribution of zoos to addressing these challenges is discussed in the next section.

The role of zoos in developing the relationship between people and biodiversity

Zoos have been considered as catalysts for conservation, recognized as partners by the scientific community for their contributions in skills and expertise that span animal care, husbandry, public engagement, education and research (Zimmermann et al. 2007; Moss et al. 2015; Gilbert and Soorae 2017). A growing commitment to biodiversity conservation has been reflected by zoos and aquariums directives, including WAZA's (The World Association of Zoos and Aquariums) pledge to contribute to meet the Aichi Biodiversity targets (Moss et al. 2015).

Zoos and aquariums are some of the most-visited institutions, with around 700 million visits globally each year. Justifications for the continued existence of zoos have evolved since their inception in the late 18th and early 19th centuries, and nearly all now position themselves as organizations focused on the conservation of biodiversity. Public education of visitors is seen as a central role in achieving this mission. Until relatively recently though, very little was known about the impacts of zoo-based education on visitors.

Moss et al. (2015, 2017) surveyed over 10,000 visitors to zoos and aquariums worldwide. Their findings indicate that:

a) People tend to end their visit with a significantly greater understanding of what biodiversity is, and the ways that they personally can help protect it.

- b) The links between these two knowledge strands were, however, found to be weaker than predicted, which leads us to question the significance of the role of knowledge in catalyzing human behavior change.
- c) The wider implication of this research is that zoos and aquariums are helping to achieve global biodiversity targets; namely, UN Aichi Biodiversity Target 1.

A follow-up survey of 161 participants revealed a further possible 'sleeper effect' resulting in the long-term increase in knowledge of pro-biodiversity actions (Jensen et al. 2017). It may be that a visit to the zoo awakens an interest in information about actions that may help biodiversity, in people's everyday lives. Therefore, the educational role of zoos should be considered as a more influential contributor to biodiversity conservation than has previously been accepted.

However, the positive effect of a zoo visit may be influenced by the way the public perceive care for animal welfare (Grajal et al. 2016; Consorte-McCrea et al. 2017a). Research also highlights the potential for unintended consequences, whereby the availability of endangered species in zoos could spark reduced interest in their conservation in the wild (Consorte-McCrea et al. 2017a). The implications of such beliefs amongst zoo visitors require further investigation.

Support for the conservation of large carnivores and for biodiversity is more likely when people have an emotional appreciation for diverse species, not just understanding. Both aspects are likely to be enhanced by direct experiences, such as visits to zoos and aquariums that provide an increasingly important opportunity for contact with other species.

Developing connection and care for nature in the zoo

The direct experiences of nonhuman animals provided by zoos have two psychologically important characteristics: they are vivid and emotionally rich, and they are typically shared with others. Vivid, emotional experiences attract more attention and they are better remembered, contributing to understanding. Social interactions surrounding zoo animals are opportunities to create and communicate shared emotional experiences and values. It is important to recognize that experiences of nature are a process, socially facilitated (or discouraged), mediated, and interpreted (Clayton et al. 2017b). Thus, the impact of a zoo visit is determined not only by the visitor's exposure to animals but by a social context that directs attention toward particular features, encourages conversation among the visitors, and endows the animals with socially-sanctioned value.

Research in several Parisian zoos examined the experience of a zoo visit, to investigate the zoo's ability to promote conservation concerns and to explore the complexity of such a visit, beyond the presumed connection among captive wild animals, visitors, and wildlife conservation issues (Figure 1). One study compared attitudes toward biodiversity among visitors to urban zoos with those of visitors to other urban parks, finding that zoo visitors reported higher concern about biodiversity, and that the frequency of zoo visits was correlated with concern (Colléony 2016). A separate study found



Figure 1. Visitors contemplating large carnivores, Menagerie du Jardin des Plantes, Paris (photo by M. SaintJalme).

that people also seemed to experience the zoo visit as an experience of nature: visitors express the feeling of "being away" when visiting the zoo, and they became more receptive to other components of biodiversity (e.g. common urban birds) in addition to the presented wildlife (Colléony et al. 2017). In a third study (Clayton et al. 2017b), zoo visitors scored higher on biodiversity concern and knowledge at the end of the visit than at the start, consistent with the findings reported by Moss et al. (2015).

Although people are attracted to the zoo to see wild animals, they are more likely to report visiting a zoo for social reasons than to learn about animals, and that their satisfaction with the visit is based in part on its success as a leisure experience. Visitors declared having felt more positive than negative emotions when exiting the zoo. However, the entertainment and educational aspects of the zoo can be mutually supporting: positive emotions were more reported by visitors who said they had learnt more (Clayton et al. 2017b).

There is much room for improvement in the ability of zoos to promote conservation. A single visit does not always increase visitors' concern for wildlife conservation. In a telling example, participating in a zoo-based animal adoption program was found to be motivated more by animal charisma than by concern about endangered species (Colléony et al. 2016). This finding could be interpreted in two ways: first, zoos may need to do more to articulate the value of endangered species, especially when soliciting donations; in addition, zoos may be able to capitalize on animal charisma to encourage more support for their conservation efforts.

Zoos are important places for conservation, but their impact may be primarily indirect: zoos are places where complex and shared experiences of nature can be promoted, to increase the sense of being connected to the natural world. It is important for them to demonstrate respect, and to encourage empathy and connection toward the nature presented at their sites.

Discussion and conclusions

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Current trends indicate that the next chapter in people-wildlife interactions will see the expansion of wild populations, recolonization, conservation translocations and 'rewilding', side by side with human population increases. In this scenario, efforts to address potential conflicts and to promote coexistence and all its benefits become essential elements of biodiversity conservation. Large carnivores must occupy their rightful place in this picture and play a key role in biodiversity dynamics.

Fear of the unexpected and of the unknown are linked to conflict, while safe, mediated face-to-face experiences with large carnivores increase perception of control, reduce fear and may allow for a positive sense of excitement and amazement (see Johansson's research, Roskaft et al. 2007; Consorte-McCrea et al. 2017b). Most people will never have an encounter with a large carnivore in the wild, so their perceptions of risk will be based on mediated information or experiences in wildlife parks and zoos. Zoos can make a valuable contribution to coexistence by promoting opportunities for knowledge and emotional connections between people and carnivores. Individuals who become less fearful of coexistence with large carnivores are more likely to visit nature and to share these experiences with children, family and friends. This in turn would facilitate restorative experiences in nature, which are believed to be important for nurturing environmental concern.

While the need to act to reduce climate change and biodiversity loss are arguably the most pressing issues of our time, many people struggle to make connections between their actions and the often "depersonalized and distant" biodiversity crisis (Grajal et al. 2016: 323; Legagneux et al. 2018). Our contributions indicate that zoos are places where people make a connection through experience, emotion and social contact. Places where complex and shared experiences of nature can be promoted, contribute to the "construction of a social identity related to concerns for animals and the environment", and a sense of connection to the animals on site that is clearly associated with pro-environmental behaviors (Clayton et al. 2011; Grajal et al. 2016: 324).

The value of individual species or groups, such as carnivores, considering the importance of interconnectedness and the interdependence of each species within whole functional ecosystems, remains uncertain (Gascon et al. 2015). The most valuable aspect of the conservation of wild carnivores may be the potential to promote the protection of all biodiversity, as "ambassador species" (both "umbrella" and charismatic, Macdonald et al. 2017). The potential of carnivore species as surrogates for conservation marketing campaigns has not sufficiently been explored (Macdonald et al. 2017), and this suggests an underdeveloped area where collaboration between zoos and programs for the conservation of carnivore species could be highly beneficial to biodiversity conservation.

Finding ways to move forward

This paper is an exploratory reflection and does not intend to exhaust the subject. It rather aims to provide a catalyst for discussion that targets underexplored cooperation between large carnivore conservation programs and zoo collections, to engage the public in the urgent need to arrest biodiversity loss. Future collaborations must include both the ecological and the social-cultural dimensions of conservation. As well as investing in ways to strengthen the relationship between people and wildlife, building a relationship of trust and dialogue between conservation initiatives and distinct interest groups is paramount, and requires interdisciplinary team work (Carter and Linnell 2016; Holland et al. 2018). Ecological research alone is not enough to slow down the loss of biodiversity. Collaborations between biology professionals, social scientists and human dimensions professionals, who are better equipped to work with people, must be better funded to fill some of the gaps to address biodiversity loss.

Education, even when carried out within zoo institutions, cannot be the panacea for all conservation problems as its power is limited due to a lack of direct connection between cause and effect (Biesta 2010). Although the zoo may be a powerful facility, because of its cultural status, its impact is associated with the social context. Because of this, zoos can bring people together to talk and listen. Although the link between education with conservation and biodiversity may not be very powerful, what adults and children experience in the zoo is deep and concrete. People's accounts of their visits refer to experiences that are emotional and social, and that reflect a sense of connection with nature, in people's urbanized everyday life. Conservation initiatives should be informed by these experiences and try to build on this foundation.

Zoos also contribute to field conservation, promoting awareness and capacity building. They can help carnivore conservation programs with husbandry procedures, nutrition and veterinarian aspects, and this knowhow can help build capacity to support field conservation in different countries.

There is space for improvement. While zoos have focused visitor awareness on *ex situ* and *in-situ* conservation collaboration, messages about what visitors can do to contribute to biodiversity, including local biodiversity, through changing their behavior remain under-explored (Ojalammi and Nygren 2018). Also, as pointed by Andrew Moss, zoos must recognize the importance of social sciences collaboration in conservation: "If we don't sort out the human issues we will just be documenting the decline of biodiversity."

The focus of biodiversity conservation strategies must be to deliver long-term answers that benefit people as part of the living world (Redpath et al. 2015). By bringing people and nonhuman nature together, zoos may be well placed to convey this vision. They may provide a space where field conservation and human dimensions can combine to foster a commitment between people, from all backgrounds, and the rest of the living world, and break down key barriers to biodiversity conservation, catalyzed by the charismatic keystone species housed within their facilities. J.V.L.B. was supported by the Ramon & Cajal program (RYC-2015- 18932) from the Ministry of Economy, Industry and Competitiveness.

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SHORT COMMUNICATION



A rapid assessment of hunting and bushmeat trade along the roadside between five Angolan major towns

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Abstract

Hunting and related bushmeat trade are activities which negatively impact wildlife worldwide, with serious implications for biodiversity conservation. Angola's fauna was severely decimated during the long-lasting civil war following the country's independence. During a round trip from Lubango (Huíla province), passing through the provinces of Benguela, Cuanza sul, Luanda, Bengo and finally to Uíge, we documented a variety of bushmeat trade, mainly along the roadside. This included snakes, rodents, duikers, antelopes, bush pigs, small carnivores and bird species. Despite being considered a subsistence activity for inhabitants in rural areas, it is concerning due to the increasing number of people becoming dependent on bushmeat trade for income generation and demand for bushmeat in the main cities. There is an urgent need to assess the impact of this activity on wildlife populations, in order to create alternative sources of income in rural areas and more effective policies focused on effective conservation of the rich biodiversity of Angola.

Keywords

Hunting, wildlife, rural areas, conservation

Introduction

Hunting of wild animals has been practised by humans for millions of years ago (Gaudzinski 2004). Consumption of bushmeat, besides being an important source of protein for households, has implications for food security and income generation for millions of people in tropical areas (Nasi et al. 2008). Bushmeat hunting and consumption have substantially increased in rural and urban areas, driven by rapid growth of the human population, easy and safe access to forests and for-profit bushmeat trade, taste preference and lack of alternative meat sources (Davies 2002; Nasi et al. 2008; Chaves et al. 2019). However, the extraction of wildlife for subsistence and commercialisation has become a major biodiversity threat in recent decades, with over-exploitation reported to be the second most important driver of change and biodiversity loss globally (IPBES 2019).

This problem is particularly relevant for Angola, where most of the wildlife was decimated during decades of post-independence civil war, as well as in conservation areas (Huntley 2017; Daskin and Pringle 2018). The country is, however, considered one of the richest and most biodiverse in Africa, accounting for an estimated 6850 native and 226 non-native plant species (Rejmánek et al. 2016; Goyder and Gonçalves 2019). Birds account for 940 species with many endemic species (Mills 2018), amphibians and reptiles accounting for 117 and 278 species, respectively (Marques et al. 2018). These numbers are expected to increase, as species new to science are still being discovered or rediscovered (Ceríaco et al. 2018; Marques et al. 2019; Vaz Pinto et al. 2019). Freshwater fishes account for 358 species, of which 22% are endemic (Skelton 2019) and 275 species of mammals are historically recorded, with new additions from recent surveys of the upper Okavango (Cubango) catchment (Taylor et al. 2018).

The long-lasting civil war contributed to an acceleration in the loss of wildlife in Angola as mentioned above, with illegal poaching leading to near extinction of many large-bodied species, including the charismatic and critically endangered Giant sable antelope (Hippotragus niger variani) (Vaz Pinto et al. 2016). Still, after more than 15 years of peace and political stability in the country, hunting and the bushmeat trade are still threatening wildlife in Angola. Protection of wildlife in Angola was regulated for many years by outdated colonial laws (e.g. Regulamento de Caça, approved by the Diploma Legislativo No. 2873, 11 de Dezembro de 1957). This document covers, in general, all aspects related to conservation and utilisation of wild animals (Huntley 1974). From there, the legislation for wildlife protection has been updated sequentially over time; for instance, all the species listed in Appendix I of CITES, to which Angola is a recent signatory, are prohibited from hunting (Decreto Executivo No. 469/15, 13 de Julho de 2015). Joint legislation between the Ministries of Finance and Agriculture fixed fines for wild animals whose hunting is prohibited in Angola and those whose hunting is permitted only during each hunting season (Decreto Executivo Conjunto No. 201/16, 26 de Abril de 2016). Other recently approved legislation establishes guidelines to ensure the conservation and sustainable use of forests and wildlife and provides a general basis for all activities related to them (Lei de Bases de Florestas e Fauna Selvagem No. 6/17, 24 de Janeiro de 2017).

Despite this legal context and governmental efforts, presently, wild animals are hunted throughout the year and the obtained bushmeat is commonly observed being sold along the roadside in the absence of an efficient law enforcement mechanism by the forestry authorities, thereby challenging the protection and conservation of wildlife in Angola. Thus, with this study, which resulted from a recent assessment along the main road between five major Angolan towns, we aimed to contribute with data on hunting and bushmeat trade.

Material and methods

The assessment of bushmeat trade was conducted between 19th–23rd September 2018. We travelled approximately 1237 km south-north, starting from Lubango, the capital city of Huíla province to Luanda and finally to Uíge province (Fig. 1). During the trip, we documented and recorded data on hunting and bushmeat trade along the roadside. The species being sold were locally identified, counted, photographed and the localities were georeferenced. The identification of species was later confirmed, based on local expertise and on the available literature (Chris 2006; MINAMB 2009a; Kingdon and Hoffman 2013).

Results and discussion

During the rapid assessment, we documented a variety bushmeat in fresh state, smoked, non-quantified dried meat and live animals, being sold mostly to urban dwellers travelling between the main cities (Table 1). Despite the recent Ebola outbreak in the neighbouring country of Democratic Republic of Congo (DRC), individual animals appear to be obtained directly from hunters and slaughtered without any sanitary measure or observing a quarantine period. This observation is particularly concerning as Uíge province shares an extensive terrestrial border with DRC and the consumption of wildlife in Africa is frequently associated with increased risk of acquiring zoonotic diseases (Ordaz-Nemeth et al. 2017).

Most of our records were documented along the main road between the Angolan provinces of Bengo and Uíge; these included many species of duikers (*Sylvicapra grimmia, Cephalopus monticola*), monkeys (*Cercopithecus mitis, Chlorocebus aethiops, Miopithecus talapoin*), snakes (e.g. *Psammophis mossambicus, Python natalensis, P. sebae*) and a globally protected species of pangolin (*Manis tricuspis*) (Fig. 2). Small antelopes, such as blue and yellow backed duikers, still represent the most hunted species and are sold along the Angolan roads (Bersacola et al. 2014).

We did not find any evidence of cross-border trade with neighbouring countries, as our survey was concentrated on the evaluation of activity along the road linking the provinces covered by this study and restricted to only a few days of driving. However, there may be trade of wildlife meat in the informal markets of the principal border



Figure 1. Map of Africa showing the location of Angola (left) and the provinces covered by the study along the main road from Lubango (Huíla province) to Uíge (right).

posts, due to the intense and unregulated commercial activities between the two countries. During this study, we witnessed a Chinese customer looking for pangolins in one of the villages; pangolin scales, when soaked, are trusted for having medicinal properties for a large variety of human illnesses mostly in Asia, but also increasing in Africa (Soewu and Adekanola 2011; Katuwal et al. 2013). It is currently estimated there are 0.4–0.7 million pangolins hunted annually, representing an increase of around 150% only for medicinal purposes over the past four decades (Ingram et al. 2018).

We also observed the sale of wading birds and parrots near Kifangondo, the main point of entrance to the capital city of Angola (Luanda) for people coming from the northern parts of the country. The number of documented species decreased from Luanda southwards. Few selling points of dried and fresh meat of rocky dassies (*Procavia capensis*), snakes (e.g. *Python natalensis*), the common (grey) and blue duikers and live species of guineafowls (*Guttera pucherani*) were recorded between Cuanza sul and Benguela. We believe that bird species, including parrots, are mostly sold as pets. In the city of Luanda, bird species, such as parrots, are commonly being sold in pet shops, fairs, along the streets and entry points to the main cities by young boys (*pers. obs.*). Bushmeat and trade of wildlife are becoming widespread commercial activities also in Angola, with serious implications on wild animal populations (Swensson 2005).

The sale of wildlife decreased substantially with only occasional observations between Benguela and Lubango (in Huíla province). This observation however cannot be



Figure 2. Wild animals and smoked bushmeat on sale along the roadside of the Sequele village, between Bengo and Uíge provinces **A** Blue duikers, Talapoin and Vervet (green) monkey in the cage on ground **B** Northern Rock Python and **C** Tree pangolin.

seen as an indication of biodiversity decline in these areas. Historically, large mammals from this vast territory of south-west Angola were deliberately eliminated to make way for cattle ranching, supported by the Declaration of Free Hunting in Huíla District (Huntley 1974). Nevertheless, additional studies are required to assess any evidence pointing to the reduction of wildlife in this region, during the post-independence period of civil war. According to Lindsey et al. (2015), illegal hunting appears to spike during periods of political instability and poor governance, due to breakdown of law enforcement and increased dependence of people on natural resources for survival.

Although there is an effort from the Angolan authorities and progress has been made in terms of legislation, unfortunately, there is no clear definition which governmental department is responsible for the protection of wildlife and what their role is. In 2009, the Angolan Ministry of Environment produced a list of species whose hunting and trade are prohibited in Angola; this included five species from our recent sur**Table 1.** Observed species sold as fresh meat, smoked or live animals from the provinces of Benguela, Luanda, Bengo and Uíge and their conservation status, the (*) refers to *Python sebae* found smoked in pieces with about 12 eggs.

Group	English Name	Scientific Name	IUCN status	State of sale	Quantity	Locality
Rodents	Rocky Dassie	Procavia capensis	Least Concern	Dried	10	Culango, Benguela
	Rocky Dassie	Procavia capensis	Least Concern	Fresh	3	Culango, Benguela
Duikers	Common (Grey) Duiker	Sylvicapra grimmia	Least Concern	Fresh	7	Culango, Benguela
Birds	Crested Guineafowl	Guttera pucherani	Least Concern	Live	1	Culango, Benguela
Snakes	Southern (Rock) Python	Python natalensis	Not assessed by IUCN	Smoked	1	Keve River, Cuanza sul
Rodents	Rocky Dassie	Procavia capensis	Least Concern	Fresh	1	Culango, Benguela
Duikers	Blue duiker	Cephalophus monticola	Least Concern	Fresh	5	Culango, Benguela
Snakes	Olive Whip Snake	Psammophis mossambicus	Not assessed by IUCN	Fresh	1	Úkua; Bengo
Duikers	Common (Grey) Duiker	Sylvicapra grimmia	Least Concern	Fresh	2	Sisala village, Vista Alegre, Uíge
Snakes	Northern (Rock) Python	Python sebae	Not assessed by IUCN	Fresh	1	Sisala village, Vista Alegre, Uíge
	Northern (Rock) Python	Python sebae	Not assessed by IUCN	Smoked	1	Vista Alegre, Uíge
Monkeys	Vervet (Green) Monkey	Chlorocebus aethiops	Least Concern	Live	1	Vista Alegre, Uíge
Rodents	Greater Cane Rate	Thryonomys swinderianus	Least Concern	Fresh	1	Vista Alegre, Uíge
Horned antelopes	Bushbuck	Tragelaphus scriptus	Least Concern	Fresh	1	Vista Alegre, Uíge
Snakes	Northern (Rock) Python	Python sebae*	Not assessed by IUCN	Smoked	1	Vista Alegre, Uíge
Pigs	Bushpig	Potamochoerus larvatus	Least Concern	Fresh	1	Vista Alegre, Uíge
Cusimanses	Ansorge's Cusimanse	Crossarchus ansorgei	Least Concern	Fresh	1	Kawanga village, Uíge
Horned antelopes	Bushbuck	Tragelaphus scriptus	Least Concern	Fresh	1	Piri, Bengo
Monkeys	Blue Monkey	Cercopithecus mitis	Least Concern	Fresh	4	Piri, Bengo
Duikers	Blue duiker	Cephalophus monticola	Least Concern	Fresh	4	Piri, Bengo
Monkeys	Blue Monkey	Cercopithecus mitis	Least Concern	Fresh	1	Piri, Bengo
Pangolins	Tree Pangolin	Manis tricuspis	Vulnerable	Fresh	1	Sequele village, Bengo
Monkeys	Blue Monkey	Cercopithecus mitis	Least Concern	Fresh	1	Sequele village, Bengo
Rodents	Rocky Dassie	Procavia capensis	Least Concern	Fresh	1	Sequele village, Bengo
Duikers	Blue duiker	Cephalophus monticola	Least Concern	Fresh	4	Sequele village, Bengo
Monkeys	Vervet (Green) Monkey	Chlorocebus aethiops	Least Concern	Live	1	Sequele village, Bengo
Monkeys	Talapoin Monkey	Miopithecus talapoin	Least Concern	Live	1	Sequele village, Bengo
Civets	African civet	Civettictis civetta	Least Concern	Fresh	1	Sequele village, Bengo
Horned antelopes	Bushbuck	Tragelaphus scriptus	Least Concern	Fresh	1	Sequele village, Bengo
Monkeys	Blue Monkey	Cercopithecus mitis	Least Concern	Fresh	1	Sequele village, Bengo

vey, namely: *Tragelaphus scriptus, Sylvicapra grimmia, Cephalophus monticola, Civettictis civetta* and *Chlorocebus aetiops* (MINAMB 2009b). Another official document mentions amongst others, these species and all *Python* spp. (with exception of the Angola python (*Python anchietae*), wrongly identified as *Boa constrictor*), as wild animals whose hunting is permitted at each hunting season (which runs from 1st August – 31st December), and fixes the respective compensation fees due to the Angolan state (Decreto Executivo No. 201/16, 26 de Abril de 2016). Surprisingly, from the above mentioned species, only *C. civetta* is included in the recent published Red List of Angolan species with the status of vulnerable (MINAMB 2018). This situation emphasises the need for an up-to-date assessment of wildlife in Angola and to produce appropriate legislation with specific actions focused on the effective protection of vulnerable species and others species currently under pressure due to illegal hunting.

Conclusions

During this short round trip, driving from Lubango to Uíge, we documented a variety of wildlife and bushmeat trade along the roadside. The actual quantity of bushmeat sold may be larger than documented in this study and may be dependent on day of week, time and season. Quantitative data on exploitation of bushmeat in local communities of Angola are scarce and its impact on wildlife populations is not currently assessed. A number of species, documented in our study, are prohibited for hunting and sale in the country, for others whose hunting is allowed, their conservation status is not domestically assessed and is instead based on global assessments. Further studies are required to assess and better evaluate the situation of species; particularly the most frequently hunted species and, based on this, to establish their conservation status locally within Angola.

Despite the progress made in terms of legislation amongst different ministerial departments, there is no clear definition of tasks and responsibilities amongst them; this resulted, for instance, in the absence of an agreement in terms of prohibited species for hunting and trade and in the inefficiency of government authority, which has resulted in uncontrolled hunting and trade of wild animals. We believe that the establishment of a forestry or wildlife authority is crucial to reduce pressure on natural resources (incl. wildlife) and in creation of more specific legislation, aiming to effectively protect wildlife in Angola.

Along our way, we did not observe any action aiming to discourage this activity from the various police checkpoints we passed. Based on this observation, we recommend strengthening enforcement measures along the main roads to alleviate pressure on wildlife due to the demand for bushmeat and other forest goods in the cities and to increase education amongst police officials in rural areas of the damage caused by bushmeat trade. Additionally, we recommend stronger enforcement to prevent any transboundary trade of bushmeat and the associated risk of acquiring diseases related to consumption of wild animals. It is also recommended that there is additional evaluation of bushmeat trade across the informal markets in the main country border posts and other larger markets of the principal cities such as Luanda, to better evaluate the dynamics of bushmeat trade across the region.

Illegal hunting and associated bushmeat trade constitute a concerning issue in terms of biodiversity conservation. Its impact must be studied and properly evaluated in order to study mechanisms to alleviate pressure on wildlife and demand of bushmeat for income generation in rural communities. This can be achieved by promoting breeding and consumption of domesticated meat in rural areas, mainly in northern parts of Angola to reduce overharvesting of wildlife and contribute to generation of income from other sources (e.g. selling of domestic animals and meat products).

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