Threats to Site Occupation of Carnivores: A Spatiotemporal Encroachment of Non-native Species on the Native Carnivore Community in A Human-dominated Protected Area

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Interspecific interactions of commensal non-native species such as domestic dogs and livestock with native wildlife are evident issues in protected areas (PAs). We studied spatiotemporal interactions by combining camera trap photographic sampling over three years. We used a generic multiseason occupancy and co-occurrence analysis and kernel density estimates of temporal activity. We accumulated a total of 1305 and 1557 independent photo-captures respectively for non-native and carnivore species during 26,216 trap nights. We found that non-native and carnivore species didn't show substantial changes in occupancy rate over time. Yet both kinds of species were well detected. Carnivores depicted low values of occupancy equilibrium than non-native species in seasons one and two. Domestic dogs directly co-occur with native carnivores (except with leopard in season one) while the human and livestock presence have direct (Species Interaction Factors > 1) and indirect (Species Interaction Factors close to 1) co-occurrence, respectively, with the leopard and two mesocarnivores. The leopard cat was the least spatially influenced carnivore by the non-native species interactions. Furthermore, the leopard had higher temporal overlap (high Δ_4) with all non-native species than the leopard cat and red fox (low Δ_4). Our study exposes the negative impact of free-ranging non-native species across this protected area on native carnivore occupancy. An

evaluation of the interconnections among non-native and carnivore species across diverse PAs management regimes is crucial to develop robust landscape-scale conservation strategies.

BACKGROUND

Protected Areas (PAs) are the most widely-known and well-accepted strategy for protecting ecosystems and biodiversity (Chape et al. 2005; Dudley 2008; Mwakatobe et al. 2013). Protected areas have proven to be effective in protecting species' habitats from land-use changes occurring outside of the protected areas (Andam et al. 2008). They represent one of the most significant global surface areas dedicated to a common goal (after areas used for food production), that of preserving global biodiversity (Palomo et al. 2014). In their regular management, PAs typically face many difficulties (Cromsigt et al. 2013; Zaman et al. 2020). One of the most common issues is human interactions with wildlife, which can be manifested in different forms (Treves and Karanth 2003; Okello et al. 2014) and often generates misunderstandings between PA managers and the local population. Carnivores need large living spaces for their daily activities, which include hunting and walking (Treves and Karanth 2003). To meet these needs, large carnivores typically use resources outside of PAs (Hansen et al. 2002; Treves and Karanth 2003), potentially bringing them into contact with human land-use activities such as livestock and crop production (Morehouse and Boyce 2017). Conflicts between non-native and native carnivore species can lead to large-scale ecosystem disturbances.

The presence of non-native species in PAs poses a threat to native carnivorous species in both space usage and temporal activities. The human activities within and around PAs generate within landscapes the presence of domestic dogs (Farris et al. 2017) and livestock species (Vanak and Gompper 2010) with harmful consequences on wildlife. The most cited effects of this include carnivores preying upon invasive livestock (Treves and Karanth 2003), causing non-native species to destabilise (Morehouse and Boyce 2017), and to spread diseases to native carnivore species in the PAs (Okello et al. 2014). They also create edge effects and habitat fragmentation (Gerber et al.

2012a; Sleeman 2013; Vanak et al. 2013; Brodie et al. 2015; Chanchani et al. 2016). Non-native species (especially when they are carnivores) often significantly strengthen pressure on native carnivores by modifying their spatiotemporal activity patterns and habitat use (Gerber et al. 2012b; Farris et al. 2015) and decreasing prey availability (Young et al. 2011). When non-native species are livestock, native carnivores can alter their natural diet because herds will seem easy prey (Okello et al. 2014; Ciucci et al. 2018). Cited effects (disease transmission, spatio-temporal destabilisation, prey decrease, preying on livestock) can be the source of imbalance of carnivore survival within the habitat and generate negative consequences on the whole landscape with the reduction of the carrying capacity in the ecosystem. Carnivores are greatly sensitive to disturbances inside and outside of PAs and are negatively affected by edge effects and human presence (poaching or human-wildlife conflict) occurring around PAs (Wearn et al. 2012; Sleeman 2013; Hua et al. 2020). Therefore, carnivore population wellbeing is expected to be driven by species-specific tolerance to micro-environment change, habitat fragmentation and PA edge effects, human presence, non-native species density, and prey availability. All these facts are essential in and around PAs and must be well managed to ensure species sustainability (Farris et al. 2017).

The Tieqiaoshan Provincial Nature Reserve (TPNR) contains some of the largest North China leopard (*Panthera pardus japonensis*, Gray 1862) populations within China (Vitekere et al. 2020a; Zhu et al. 2021). While most of the extant North China leopard population is hosted within 22 Nature Reserves situated in the Taihang Mountains and some nearby regions (Song et al. 2014), most of these PAs have not been surveyed and accurate population estimates are lacking.

Thus, little is known about this leopard sub-species living in a guild with two mesocarnivores, the leopard cat (*Prionailurus bengalensis*, Kerr 1792) and the red fox (*Vulpes vulpes*, Linnaeus 1758) within the TPNR ecosystem (Hua et al. 2020). This landscape hosts a considerable human population density (local people), with livestock activities generating the invasion of the integral conservation zone of the TPNR by dogs, livestock, and humans (*e.g.*, Farris et al. 2017). There has been a scarcity of studies of the conservation status of these carnivores and the effects of non-native species introduced by the shepherds in the PAs. Hua et al. (2020) highlighted the effect of human presence on the detectability of these carnivores. Still, the long-term effect and the coexistence with non-native species remain unstudied within the TPNR landscape.

We carried out a multi-year study of the coexistence between non-native species: the domestic dog (dog), livestock and herdsmen (human), and native carnivores: North China leopard (leopard), leopard cat and red fox (fox) within one of the Taihang Mountains landscapes, the TPNR. We first hypothesized that carnivores would not depict the stability of occupancy contrarily to non-native species' over the years. We also hypothesized that all three native carnivores would have a real coexistence defined as "apparent co-occurrence" or "direct interaction" with non-native species, and

they would portray increasing Species Interaction Factors (SIF: a parameter describing the spatial interactions of two species in an area, previously computed by Alexander et al. (2016) and Farris et al. (2020)) over the years. Human detection, particularly, would markedly affect native species since the two others (livestock and dog) are human presence-dependent. We finally hypothesized that non-native and carnivore species would not temporally overlap by assuming non-native and native carnivore species being respectively diurnal and nocturnal.

Studying these multi-year spatiotemporal interactions in a landscape with human invasion (bringing invasive species) will allow the effectiveness of management policies for these carnivores species conservation in the TPNR to be assessed. The findings of this work will provide further suggestions to improve strategies for sustainable management of PAs hosting non-native species.

MATERIALS AND METHODS

Study Area

The TPNR is one of the reserves hosting the North China leopard sub-species in China. This PA has GPS coordinates: 111°25'E to 114°17'E and 36°39'N to 38°06'N (Fig. 1) with the elevation ranges from 1300 to 1827 m. The TPNR is a Protected Area, approved by the provincial administration by the document No.124. Officially invested in 2009, this PA was assigned a total of 353.52 km^2 (Zhu et al. 2021) divided into an area of integral protection (139.5 km^2), a buffer zone (74.2 km^2), and a multi-use zone. The annual average of rainfall varied from 500 mm to 700 mm, with heavy rains in the period July-September (Hua et al. 2020). This area did not present high daily and yearly thermal amplitude, with respectively 10°C and 6°C as mean temperatures (Zheng et al. 2009). One of the principal characteristics of this PA was to host humans (Zhu et al. 2021) with the total number of inhabitants estimated to be approximatively to two thousand and the PA had always experienced disturbances from this human population (Hua et al. 2020). A significant part of the area was a mixture of primary and secondary forests and the remaining parts are shrubs. Wildlife was abundant within the PA, including mammals (carnivores: leopard, leopard cat, fox, badger, etc.; artiodactyl: many kinds of deer and the wild boar), diversified fauna of reptiles, amphibians, and birds (Song et al. 2014).
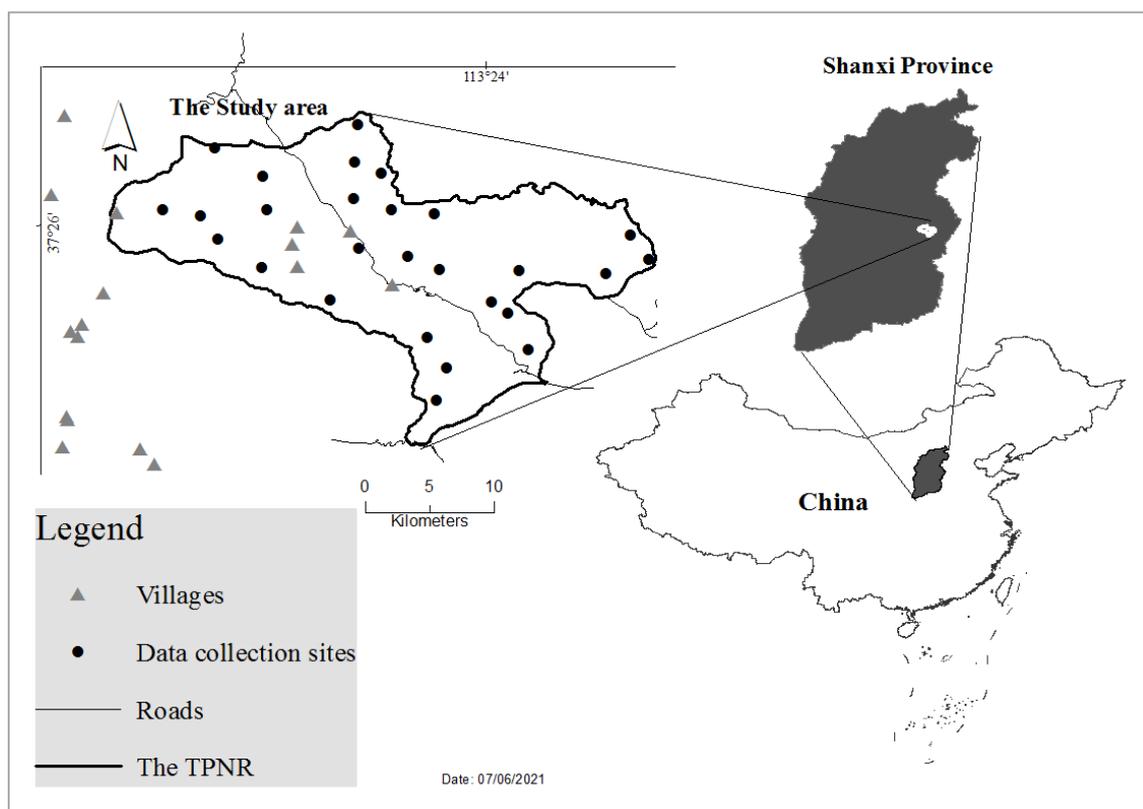
Fig. 1. The data collection sites within the Tieqiaoshan Provincial Nature Reserve and villages housing herdsmen in and around the Protected Area.

Methods

Data Collection

We collected data on the presence and absence of three native carnivore species and three non-native species for a total of 383 days over 3 years: 130 (March–July 2017), 119 (September-December 2018) and 134 (March-June 2019), giving 3 sampling periods (SP$_1$, SP$_2$, and SP$_3$) and 2 interseasons (IS$_1$ and IS$_2$), according to Farris et al. (2017). We used 2 brands of cameras: the Eastern Red Hawk E1B 6210M (Shenzhen Ereagle Technology Co.Ltd, Shenzhen, China) and the LTL6210MM (LTL Acorn Trail Camera, United Kingdom). Both brands were triggered remotely by an infrared sensor to record animal activity, following Karanth et al. (2003) and Swann et al. (2011). SP$_1$ used 81cameras while SP$_2$ and SP$_3$ used 62 cameras. Cameras were deployed within 27 4 km $\times$ 4 km quadrants in the study area, attached to trees at an average height of 0.5 m. Each data collection site had 2 or 3 cameras installed to face each other. Where possible, cameras were placed on trails, but otherwise they were placed at points thought to maximise the visibility of the animals. Cameras were set to capture data with the time and date automatically displayed on the photos (*e.g.*, Barull et al. 2014). Each camera operated for at least 100 consecutive days in each sampling period.

Data Analysis

Spatial patterns

We first aggregated data from more than 100 days of capture within each sampling period into multiple shorter intervals. In SP_1 and SP_3, we considered 2 weeks as one survey (sampling occasion) while 10 days were combined as one survey for SP_2. This data aggregation allowed standardisation of the 3 sampling periods (*e.g.*, Bu et al. 2016; Farris et al. 2017) and provided multiple surveys within each sampling period, as required for occupancy modelling (Alexander et al. 2016; MacKenzie et al. 2006). We considered a species to be detected if it was present at a site in an interval of aggregated days. Otherwise, it was not detected.

We then computed 2 different occupancy analyses to investigate interactions between native carnivore and non-native species: the multiseason occupancy and the multiseason co-occurrence analyses. Occupancy analysis is based on collecting occurrence data of studied species within data collection sites. Species can be imperfectly detected; therefore, *n* sites are visited on *t* sampling occasions, and the presence/absence of each targeted species is recorded on each occasion (MacKenzie et al. 2003). We used the software PRESENCE (version 5.8 < 130315.0823 > by James E Hines). This modelling using presence/absence data of different species allowed us to estimate changes in occupancy of all species over three years to test if there is an apparent spatial co-occurrence between native carnivores and non-native species, and finally to assess the influence of non-native species on the occupancy and detection probabilities of native species.

In the first step (multiseason occupancy), parameters estimated can depict variations across time: the probability of occupancy (ψ), the probability of detection (p), the colonisation rate (γ) and the local extirpation rate (ε), all estimate values were accompanied by their standard errors. We estimated these parameters to determine the general trend of site occupation of species across years. Following MacKenzie et al. (2006), two derived parameters were also computed for the interpretation of the occupancy dynamics: (1) the rate of change in occupancy:

$$\lambda'_t = \frac{\psi_{t+1}/(1-\psi_{t+1})}{\psi_t/(1-\psi_t)} \qquad \text{(eq}_1 \text{ MacKenzie et al. 2006)}$$

(2) the occupancy equilibrium:

$$\psi_{equilibrium} = {\gamma}/{(\gamma + \varepsilon)} \qquad \text{(eq}_2 \text{ MacKenzie et al. 2006)}$$

In the second step (multiseason co-occurrence), we computed the co-occupancy and co-detection parameters (Table 1), and the SIF (φ). This latter parameter describes the species' interactions in an area, where $\varphi < 1$ indicates no interaction or avoidance, $\varphi > 1$ indicates direct interaction or apparent co-occurrence and $\varphi = 1$ indicates independent or indirect co-occurrence

(Alexander et al. 2016; Farris et al. 2020). We then used the Chi-squared test of independence to verify if the occupancy of a carnivore computed as single species is independent from the same species' occupancy in a co-occurrence (two species) pattern.

Table 1. Parameters computed in the multiseason co-occurrence models to verify the effect of the invasive species' presence on the occupancy, detection, colonization, and local extirpation of carnivores in the Tieqiaoshan Provincial Natural Reserve, (Par: Parameters)

Par	Definitions
ψ^{BA}	The probability that species B initially occupies the area, given that species A is also present
ψ^{Ba}	The probability that species B initially occupies the area, given that species A is not present
γ^{BAA}	The probability that the area is colonised by species B in the interval t, t+1, given that species A is present in survey t and species A persists in the interval t, t+1
γ^{BAa}	The probability that the area is colonised by species B in the interval t, t+1, given that species A is present in survey t and species A goes extinct in the interval t, t+1
γ^{Baa}	The probability the area is colonised by species B in the interval t, t+1, given that species A is not present in survey t and species A does not colonise in the interval t, t+1
ε^{BAA}	The probability that species B becomes extinct in the area in the interval t, t+1, given that species A is present in survey t and species A persists in the interval t, t+1
ε^{BAa}	The probability that species B becomes extinct in the area in the interval t, t+1, given that species A is present in survey t and species A goes extinct in the interval t, t+1
ε^{Baa}	The probability that species B becomes extinct in the area in the interval t, t+1, given that species A is not present in survey t and species A does not colonise in the interval t-t+1
r^{BA}	The probability of detecting species B, given that both are present and species A detected
r^{Ba}	The probability of detecting species B, given that both are present and species A not detected
φ	Species Interactions Factor (SIF)

Temporal patterns

The time that a species was captured was automatically stamped on species photographs. We removed any subsequent photos of the same species at the same site that occurred within 30 minutes to minimize pseudo-replication biases (*e.g.*, Monterroso et al. 2013; Sunarto et al. 2015; Farris et al. 2017). All photos of a species remaining in the dataset after the application of this filter were considered to be independent observations. We compared the day and night visibility of species by calculating the proportion of detections that occurred in two intervals: 06:00–18:00 for daytime and 18:00–06:00 for night-time to test the species' "nocturnality". A species was categorized to prefer night-time or daytime when its detection rate was ≥ 70%, respectively in the 06:00–18:00 and 18:00–6:00 time interval (*e.g.*, Dias et al. 2018; Hua et al. 2020). To analyze the temporal activity overlap between non-native species and native carnivore, we calculated the kernel density estimates (KDEs) using the R package overlap (Oliveira-Santos et al. 2013; Meredith and Ridout 2014). We assessed the temporal overlap coefficient (Δ_4) to compare activity patterns of all pairwise species combinations of non-native species and native carnivores. The overlap coefficient is a metric that ranges from zero, meaning the absence of overlap, to one, meaning complete overlap (Linkie and Ridout 2011; Meredith and Ridout 2014). As our sample was large (*n* > 75), we estimated the overlap coefficient using the estimator Dhat4 (*e.g.*, Guerisoli et al. 2019) denoted by Δ_4. We

computed the 95% confidence interval (hereafter, 95% CI) from 999 bootstrap samples to obtain this estimator's precision (Dias et al. 2019; Mori et al. 2020). The species' overlap coefficient was considered low if $\Delta_4 < 0.50$, intermediate if $0.50 < \Delta_4 < 0.70$, and high if $\Delta_4 > 0.70$ (*e.g.*, Monterroso et al. 2014).

The spatiotemporal value (STV) for species' interactions

We emphasized on conducting an approach to explore species' spatiotemporal overlap, which was depicted with both non-native species and native carnivores within the study area. At this end, we made a combination of results from spatial patterns; multiseason two-species co-occurrence analysis and the temporal activity overlap between these two kinds of species. The first parameter used was the SIF. We combined it to the temporal overlap coefficient (Δ_4) performed from the kernel density estimator. Both SIF and Δ_4 are probabilities, thus the probability of SIF "and" Δ_4 will imply multiplication. Therefore, we computed the STV by multiplying the SIF value by the Δ_4 value *i.e.*, STV = SIF * Δ_4, as previously used by Farris et al. (2020). These two parameters (SIF and Δ_4) varied between the different paring species (non-native species and native carnivores). This combination was useful to perform as it is not obvious to differentiate the site in which species have a temporal activity overlap. Also the spatial co-occurrence analyses of species can display bias particularly when considering that investigated sites may be occupied by one or both species (for the paring species used), but these two species can be undetected. Such cases can imply the imperfection detection concept of MacKenzie et al. (2006). Accordingly, the STV shows the degree of overlap for each species pairing, thus 0 would designates no overlap for both spatial and temporal patterns and as the STV rises this confirms the aggregation of spatial and temporal overlap, which depicts direct interactions between species (Farris et al. 2020).

RESULTS

Overall Trend of Capture and Multi-Year Changes in Species Estimates

For non-native species, investigations in the TPNR produced over the three seasons a total of 526, 631 and 145 independent photographs for human, livestock, and dog, respectively. For carnivore species, there were 128, 154, and 412 independent photos respectively for leopard, leopard cat, and fox. In total, for survey duration of 383 days and 205 cameras, there were 26,216 trap nights. The overall trap success rates (which is the total number of independent captured

photographs for a species divide by the total number of night-traps) for non-native species were respectively 2.01%, 2.40% and 0.55% for human, livestock, and dog; and 0.48%, 0.58%, and 1.57% for leopard, leopard cat, and fox.

Spatial Multi-Year Patterns

For the multi-year occupancy estimates for non-native species, livestock had the highest occupancy of 0.78 ± 0.06 in SP_2 followed by human with 0.61 ± 0.03 in the SP_1, which also had the lowest site occupation among all non-native species (0.43 ± 0.09) in SP_2. The dog had 0.53 ± 0.10 as highest site occupation estimates in SP_3 (Fig. 2). The leopard cat showed the highest probability of site occupation for carnivores, particularly SP_3, with 0.82 ± 0.11. The fox had the second-highest site occupation probability of 0.74 ± 0.08 in SP_1. In the previous study (Vitekere et al. 2020b), the leopard depicted an average site occupation probability with its highest estimate found in SP_1 (0.54 ± 0.09). The lowest value found was for the leopard (0.44 ± 0.10) in SP_2 (Fig. 2). Neither non-native nor native carnivore species showed a substantial rate of change in occupancy (all values < 2, Table 2). However, carnivores had relatively low occupancy equilibrium values than non-native species in IS_1 (Table 2) except human represented by the lowest value of 0.22 (Table 2) when the pattern in IS_2 was different. The dog was the only species found at equilibrium in both IS according to its equilibrium occupancy values. Yet the fox show also an equilibrium in the SP_2 (Table 2).
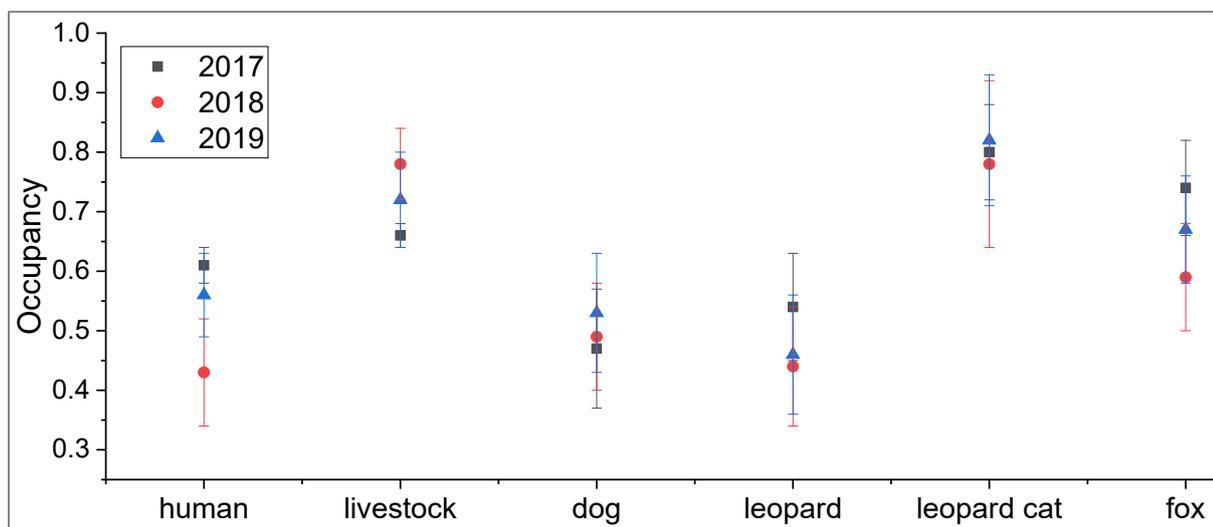

Fig. 2. Estimated site occupation probability across three years (2017–2019) of non-native species (human, livestock and dog), and carnivore species (leopard, cat and fox) in the Tieqiaoshan Provincial Natural Reserve, outputs of multi-year analysis computed in PRESENCE software. Carnivores' data have been previously used by Vitekere et al. (2020b).

Table 2. The occupancy equilibrium and rate of change in occupancy of non-native species (human, livestock, and dog) and carnivore species (leopard, cat, and fox), computed as derived parameters from equation one (eq$_1$) and equation two (eq$_2$), respectively, to show trends in species occupancy from 2017 to 2019 in the Tieqiaoshan Provincial Natural Reserve.

Species	OE$_1$	RC$_1$	OE$_2$	RC$_2$
human	0.22	0.48	0.52	1.68
livestock	0.58	1.82	0.45	0.72
dog	0.70	1.08	0.79	1.17
leopard	0.55	0.96	0.45	1.08
leopard cat	0.36	0.88	0.56	1.28
fox	0.49	0.5	0.69	1.41

OE: occupancy equilibrium and RC: rate of change in occupancy, one and two are IS$_1$ and IS$_2$.

In general, the fox had the highest detection probability, followed by human. The lowest detection pertained to the dog (Fig. 3). The human presence in the SP$_1$ (0.47 ± 0.03) was the highest detection probability amongst non-native species, followed by livestock (0.32 ± 0.03) in the SP$_1$. The lowest detection was for the dog (0.20 ± 0.03) in the SP$_2$. For the carnivore, the fox had the highest detection probability (0.64 ± 0.03) followed by the leopard with 0.36 ± 0.05 in the SP$_1$. The lowest detection was for the leopard cat (0.24 ± 0.03) in the SP$_2$ (Vitekere et al. 2020b).
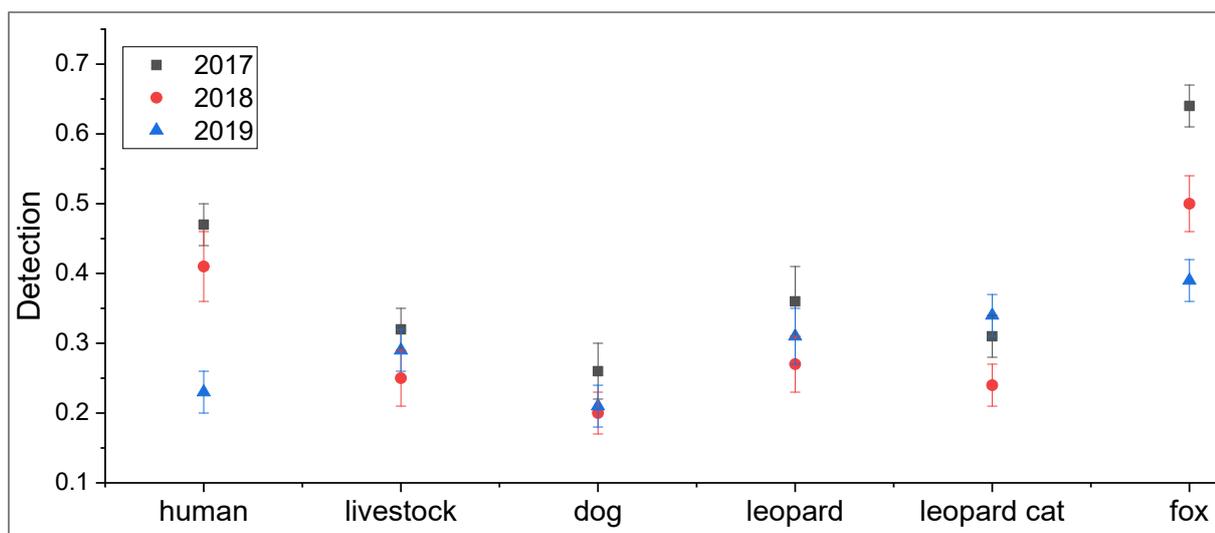

Fig. 3. Estimated detection probabilities across three years (2017–2019) of non-native species (human, livestock and dog) and carnivore species (leopard, cat and fox) in the Tieqiaoshan Provincial Natural Reserve, outputs of multi-year analysis performed in PRESENCE software. Carnivores' data have been previously used by Vitekere et al. (2020b).

The highest colonisation rates were 0.54 ± 0.15, 0.42 ± 0.12, respectively for fox and dog in IS$_2$ and 0.32 ± 0.06 for livestock in the IS$_1$ (Fig. 4). The lowest colonisation rates were in the IS$_1$ for both native carnivores and non-native species (0.15 ± 0.09 for leopard cat and 0.13 ± 0.08 for human). Two non-native species had the highest extirpation rates (Fig. 5) for both categories of species, human in IS$_1$ and livestock in the IS$_2$, respectively with 0.45 ± 0.09 and 0.30 ± 0.05. The

lowest extirpation rate was for the dog in the IS_2 (0.11 ± 0.09). The fox had the highest extirpation rate among carnivore species, followed by the leopard cat both in the IS_1 (0.29 ± 0.10 and 0.26 ± 0.15, respectively). The less extirpated carnivore was leopard within the IS_1 (0.21 ± 0.15).
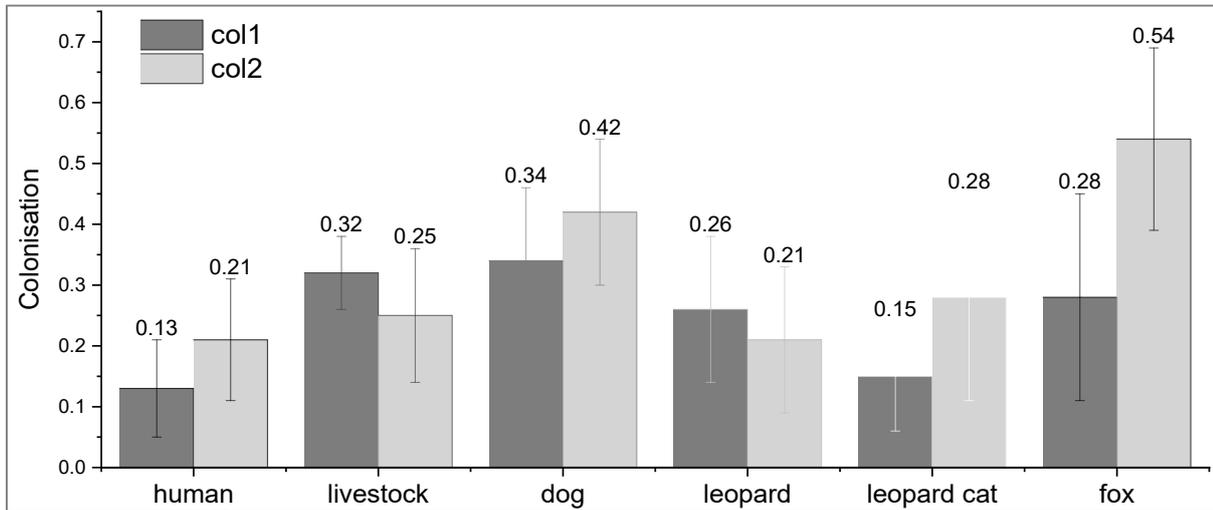

Fig. 4. Estimated colonisation rates across three years (2017–2019) of non-native species (human, livestock and dog) and carnivore species (leopard, cat and fox) in the Tieqiaoshan Provincial Natural Reserve, outputs of multi-year analysis performed in PRESENCE software, col1: colonisation in interseason 1 and col2: colonisation in interseason 2. Carnivores' data have been previously used by Vitekere et al. (2020b).

Fig. 5. Estimated extirpation rates across three years (2017–2019) of non-native species (human, livestock, and dog) and carnivore species (leopard, cat, and fox) in the Tieqiaoshan Provincial Natural Reserve, outputs of multi-year analysis performed in PRESENCE, ext1: local extirpation in interseason 1 and ext2: local extirpation interseason 2. Carnivores' data have been previously used by Vitekere et al. (2020b).
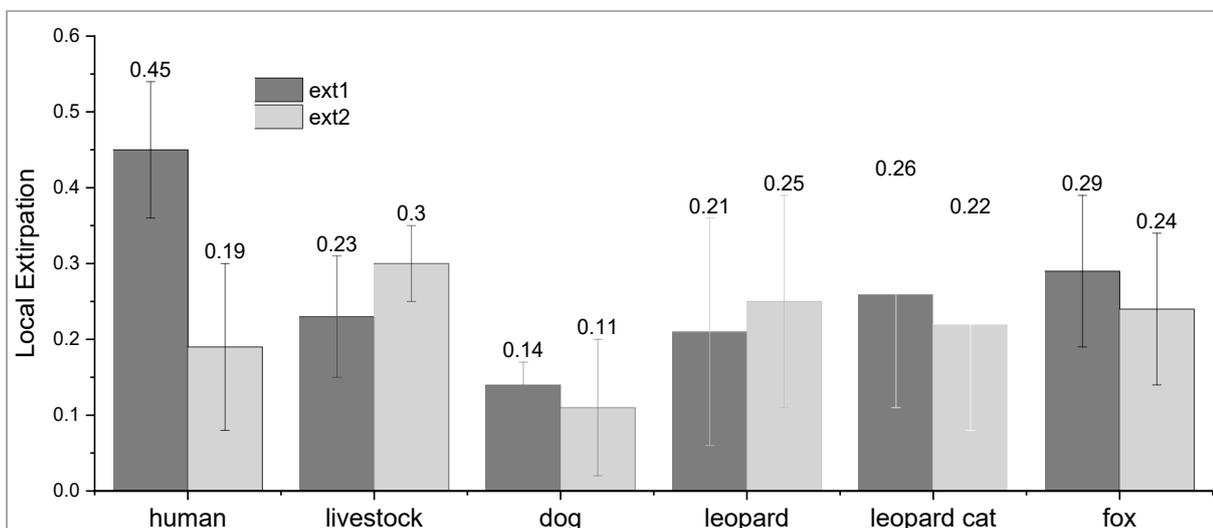
Multi-Year Co-occurrence Estimates

For all comparisons, there were no significant differences between the occupancy of a single species' analysis and the two species co-occurrence analysis as all p-values were greater than 0.05. In the human-carnivores coexistence (Table 3A), the leopard occupancy remained almost the same with human absence except in the SP_2. The leopard cat's site occupation was low in human presence except in SP_3. The fox depicted unchanged estimates for occupancy in human presence except in SP_2. Human absence respectively influenced positively and negatively the colonisation and local extirpation of the leopard and the leopard cat (except the local extirpation in the IS_2). For the fox, the colonisation slightly diminished in both presence and absence of human, and the extirpation rate remains unchanged in the human absence in both IS. Its occupancy did not change in human presence and absence for the first two SP. The human presence influenced the detectability of the leopard in all three SP. Simultaneously, the detection of the leopard cat did not markedly change in human presence, and this human presence did not influence the fox's detectability.

Referring to the livestock-carnivore interaction (Table 3B), livestock presence brought a lesser influence to the occupancy of leopard and the occupancy of the leopard cat was modified (except the SP_1) and the fox occupancy changed in the SP_3. The colonisation rates of carnivores were influenced by livestock presence, as for the leopard and the fox, their occupancy slightly changed, especially in IS_2. Surprisingly, livestock absence positively influenced the leopard's local extirpation when for leopard cat and fox, they were negatively influenced. Detection probability of leopard was lesser with livestock absence, for leopard cat and fox did not markedly change with livestock presence.

For dog-carnivore coexistence (Table 3C) the leopard and leopard cat occupancies slightly changed with dog presence when it markedly changed for the fox, especially in the SP_3. In general, the dog presence influenced the colonization rates of the leopard and fox in both IS. The dog absence impacted negatively the leopard's local extirpation, while its presence changed the local extirpation for leopard cat and fox. The detection slightly lessened for all species with the dog presence.

Table 3. Co-occurrence results for non-native species (species A) and carnivores (species B) including the species interaction factor (SIF) within the Tieqiaoshan Provincial Nature Reserve (2017–2019)

A: human-carnivores

	ψ^{BA}	ψ^{Ba}	γ^{BAA}	γ^{BAa}	γ^{Baa}	ε^{BAA}	ε^{BAa}	ε^{Baa}	r^{BA}	r^{Ba}	φ
SP											
human-leopard											
one	0.46 ± 0.09	0.58 ± 0.05	0.23 ± 0.07	0.26 ± 0.09	0.30 ± 0.10	0.29 ± 0.08	0.27 ± 0.13	0.15 ± 0.05	0.19 ± 0.08	0.30 ± 0.02	1.16 ± 0.03
two	0.42 ± 0.15	0.39 ± 0.01	0.15 ± 0.03	0.18 ± 0.06	0.22 ± 0.08	0.32 ± 0.10	0.21 ± 0.08	0.18 ± 0.14	0.20 ± 0.10	0.14 ± 0.12	1.18 ± 0.09
three	0.44 ± 0.11	0.50 ± 0.07	NA	NA	NA	NA	NA	NA	0.18 ± 0.09	0.25 ± 0.03	1.21 ± 0.10
human-leopard cat											
one	0.78 ± 0.07	0.81 ± 0.09	0.11 ± 0.04	0.20 ± 0.06	0.19 ± 0.06	0.31 ± 0.16	0.25 ± 0.08	0.23 ± 0.05	0.29 ± 0.11	0.36 ± 0.05	1.05 ± 0.11
two	0.63 ± 0.13	0.71 ± 0.04	0.14 ± 0.08	0.18 ± 0.12	0.22 ± 0.07	0.22 ± 0.11	0.19 ± 0.09	0.20 ± 0.04	0.33 ± 0.08	0.49 ± 0.14	1.08 ± 0.15
three	0.78 ± 0.11	0.67 ± 0.08	NA	NA	NA	NA	NA	NA	0.31 ± 0.10	0.30 ± 0.12	1.11 ± 0.05
human-fox											
one	0.70 ± 0.01	0.76 ± 0.08	0.21 ± 0.10	0.19 ± 0.11	0.26 ± 0.02	0.36 ± 0.06	0.31 ± 0.02	0.28 ± 0.13	0.50 ± 0.14	0.55 ± 0.10	1.05 ± 0.09
two	0.42 ± 0.09	0.58 ± 0.11	0.28 ± 0.07	0.36 ± 0.05	0.48 ± 0.03	0.32 ± 0.01	0.32 ± 0.04	0.23 ± 0.02	0.35 ± 0.13	0.48 ± 0.05	1.11 ± 0.05
three	0.64 ± 0.09	0.66 ± 0.05	NA	NA	NA	NA	NA	NA	0.26 ± 0.11	0.28 ± 0.09	1.17 ± 0.02

B: livestock-carnivores

	ψ^{BA}	ψ^{Ba}	γ^{BAA}	γ^{BAa}	γ^{Baa}	ε^{BAA}	ε^{BAa}	ε^{Baa}	r^{BA}	r^{Ba}	φ
SP											
livestock-leopard											
one	0.46 ± 0.09	0.49 ± 0.05	0.44 ± 0.02	0.24 ± 0.07	0.20 ± 0.13	0.16 ± 0.08	0.29 ± 0.02	0.28 ± 0.05	0.24 ± 0.15	0.25 ± 0.17	1.29 ± 0.02
two	0.48 ± 0.10	0.41 ± 0.09	0.39 ± 0.05	0.32 ± 0.12	0.18 ± 0.09	0.21 ± 0.05	0.24 ± 0.03	0.30 ± 0.08	0.20 ± 0.10	0.25 ± 0.08	1.34 ± 0.09
three	0.56 ± 0.08	0.45 ± 0.07	NA	NA	NA	NA	NA	NA	0.47 ± 0.08	0.19 ± 0.13	1.27 ± 0.11
livestock-leopard cat											
one	0.81 ± 0.07	0.78 ± 0.08	0.14 ± 0.08	0.28 ± 0.13	0.28 ± 0.10	0.14 ± 0.05	0.13 ± 0.08	0.10 ± 0.03	0.28 ± 0.11	0.36 ± 0.12	1.32 ± 0.07
two	0.67 ± 0.02	0.52 ± 0.08	0.17 ± 0.04	0.19 ± 0.11	0.23 ± 0.09	0.28 ± 0.07	0.23 ± 0.09	0.15 ± 0.08	0.19 ± 0.08	0.31 ± 0.10	1.08 ± 0.03
three	0.57 ± 0.10	0.46 ± 0.06	NA	NA	NA	NA	NA	NA	0.33 ± 0.10	0.32 ± 0.09	1.06 ± 0.08
livestock-fox											
one	0.76 ± 0.08	0.70 ± 0.03	0.27 ± 0.08	0.25 ± 0.05	0.30 ± 0.08	0.32 ± 0.09	0.29 ± 0.11	0.23 ± 0.07	0.66 ± 0.05	0.60 ± 0.07	1.04 ± 0.04
two	0.60 ± 0.01	0.47 ± 0.05	0.48 ± 0.03	0.50 ± 0.03	0.55 ± 0.11	0.27 ± 0.13	0.25 ± 0.08	0.18 ± 0.10	0.50 ± 0.01	0.57 ± 0.11	1.14 ± 0.09
three	0.75 ± 0.10	0.49 ± 0.09	NA	NA	NA	NA	NA	NA	0.32 ± 0.04	0.39 ± 0.06	1.10 ± 0.09

C: dog-carnivores

	ψ^{BA}	ψ^{Ba}	γ^{BAA}	γ^{BAa}	γ^{Baa}	ε^{BAA}	ε^{BAa}	ε^{Baa}	r^{BA}	r^{Ba}	φ
SP											
dog-leopard											
one	0.43 ± 0.04	0.48 ± 0.01	0.36 ± 0.08	0.39 ± 0.07	0.33 ± 0.01	0.25 ± 0.10	0.23 ± 0.05	0.18 ± 0.02	0.29 ± 0.07	0.33 ± 0.02	0.93 ± 0.02
two	0.61 ± 0.01	0.32 ± 0.05	0.20 ± 0.03	0.25 ± 0.09	0.23 ± 0.04	0.28 ± 0.08	0.27 ± 0.08	0.16 ± 0.06	0.19 ± 0.04	0.22 ± 0.08	1.36 ± 0.03
three	0.55 ± 0.08	0.31 ± 0.03	NA	NA	NA	NA	NA	NA	0.23 ± 0.08	0.37 ± 0.10	1.29 ± 0.07
dog-leopard cat											
one	0.83 ± 0.05	0.78 ± 0.01	0.16 ± 0.06	0.13 ± 0.10	0.20 ± 0.09	0.19 ± 0.07	0.23 ± 0.11	0.25 ± 0.08	0.24 ± 0.07	0.31 ± 0.08	1.17 ± 011
two	0.78 ± 0.08	0.60 ± 0.09	0.19 ± 0.04	0.28 ± 0.03	0.17 ± 0.05	0.20 ± 0.02	0.18 ± 0.05	0.21 ± 0.01	0.21 ± 0.06	0.28 ± 0.03	1.16 ± 0.05
three	0.81 ± 0.03	0.77 ± 0.07	NA	NA	NA	NA	NA	NA	0.25 ± 0.12	0.32 ± 0.09	1.13 ± 0.04
dog-fox											
one	0.83 ± 0.10	0.66 ± 0.09	0.42 ± 0.08	0.38 ± 0.08	0.29 ± 0.06	0.36 ± 0.08	0.29 ± 0.01	0.15 ± 0.06	0.58 ± 0.10	0.50 ± 0.08	1.32 ± 0.03
two	0.60 ± 0.08	0.35 ± 0.11	0.49 ± 0.03	0.56 ± 0.07	0.32 ± 0.01	0.29 ± 0.05	0.24 ± 0.03	0.21 ± 0.07	0.51 ± 0.07	0.48 ± 0.11	1.64 ± 0.08
three	0.84 ± 0.11	0.54 ± 0.13	NA	NA	NA	NA	NA	NA	0.49 ± 0.12	0.43 ± 0.08	1.47 ± 0.01

Estimates are accompanied by standard errors, SP: sampling period and NA: not applicable because colonization and local extirpation rates are only present in IS.

Temporal Patterns

All the non-native species portrayed a marked preference of daytime with very low nocturnalities (proportion of observations between 18:00 and 06:00) of 0.11, 0.12 and 0.16 respectively for human, livestock, and dog. The leopard was crepuscular with a broad peak of activity in the morning and a more sharply defined evening peak around 18:00–19:00, with a nocturnality of 0.41; the leopard cat and the fox preferred night-time with nocturnalities of 0.71 and 0.69, respectively and peak activity around midnight. Non-native species had noteworthy peaks of activity in the morning (7:00) and in the early evening (18:00), whereas they were observed less frequently around noon (Fig. 6).

The activity time overlap coefficients (Δ_4) were low for all pairwise species combinations of non-native species with the leopard cat and the fox (the highest value was 0.48 between livestock and fox). However, overlap of non-native species with the leopard was higher (human-leopard: 0.73; livestock-leopard: 0.75 and dog-leopard: 0.74, Table 4). The spatiotemporal value (STV) (Table 4) concomitantly indicates the spatial and the temporal overlapping in one value, with the highest value for the species pairing livestock-leopard (0.97) and the lowest for the pair human-leopard cat (0.41).
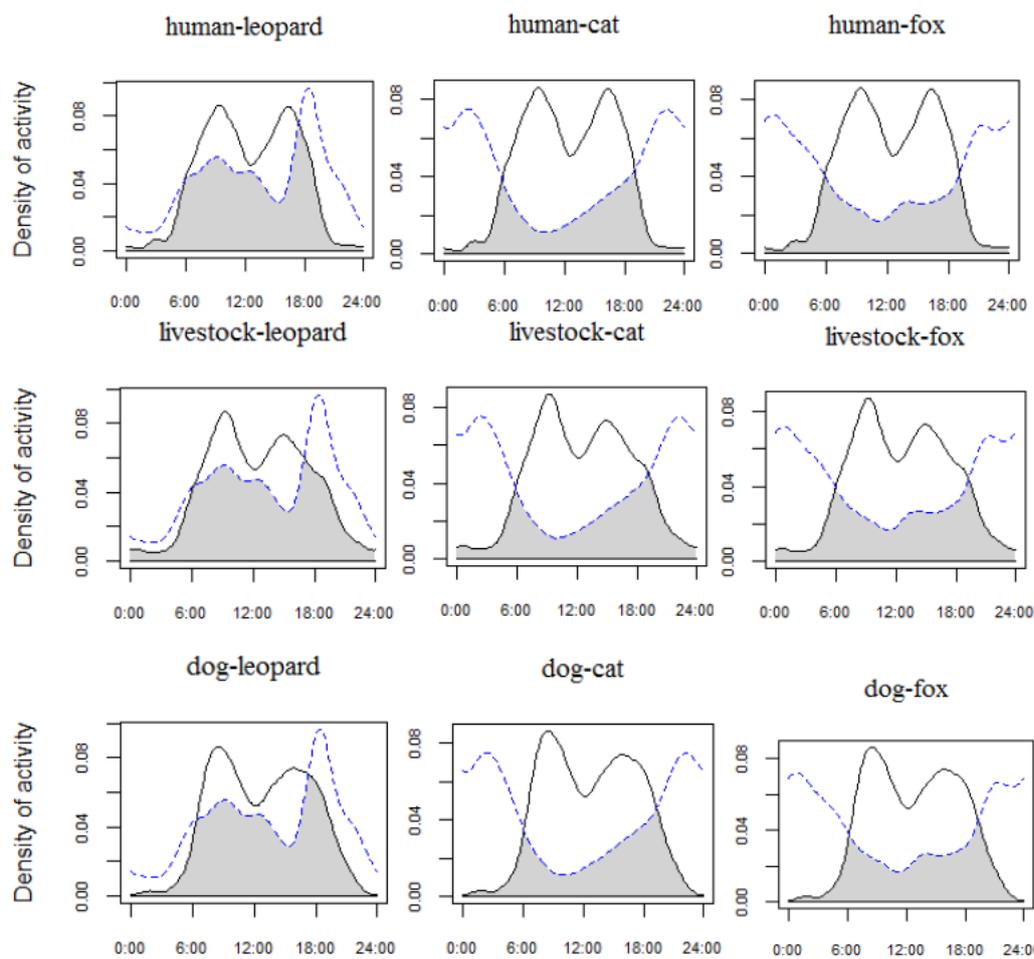
Fig. 6. Overlap of density of activity over three years between the non-native species (lines) and native carnivores species (dashed lines) based on camera trap data (2017–2019) in Tieqiaoshan Provincial Natural Reserve ("cat" represents the "leopard cat").

Table 4. Estimated activity overlap coefficient (Δ_4), associated 95% confidence interval obtained using the bootstrap method with 999 sample replications and the spatiotemporal value (STV which describes simultaneously the spatial and temporal overlap value, its obtained by multiplying the SIF by Δ_4) for non-native species and carnivores species the in the Tieqiaoshan Provincial Nature Reserve (2017–2019)

Species pairwise	(Δ_4)	95% CI	Average STV
human-leopard	0.73	0. 64-0.80	0.86
human- cat	0.38	0.31-0.45	0.41
human- fox	0.42	0.37-0.47	0.46
livestock-leopard	0.75	0.37-0.83	0.97
livestock- cat	0.44	0.37-0.51	0.50
livestock- fox	0.48	0.44-0.53	0.52
dog-leopard	0.74	0.64-0.82	0.88
dog- cat	0.39	0.31-0.48	0.44
dog-red fox	0.44	0.37-0.50	0.64

DISCUSSION

Overall Species' Site and Time Occupation Patterns

Among all non-native species, livestock depicted the highest occupancy across all SP, followed by humans in SP_1 and SP_3 and the dog had the lowest. The non-native species were predominantly diurnal with very low nocturnality (close to 10%). Except for the leopard which intensely selected crepuscular time, carnivore species preferred the night for their diel activity time. As well known, humans always prefer daytime for their activities (Mori et al. 2020), inducing some invasive species (dog and livestock mainly) to have a similar pattern of time activity as they are mostly human-dependent (Vanak and Gompper 2010; Farris et al. 2015; Farris et al. 2016; Farris et al. 2017). The presence of the non-native species was quantified by their occupancy estimates (> 0.40 for all species) that indicated how these species are permanent in PAs, although human activities are forbidden in most declared conservation ecosystems (Chape et al. 2005; Dudley 2008). Non-native species remain real threats to wildlife (Gerber et al. 2012a; Sleeman 2013; Vanak et al. 2013; Brodie et al. 2015; Chanchani et al. 2016). Concomitantly, native carnivore site occupation was evident (lowest occupancy was 0.44) in the area, with the leopard cat having the highest occupancy across all SP (Fig. 2). The fox showed higher occupancy than the leopard and was captured mainly at night-time. Commonly, carnivores are reputed to be nocturnal (Schuette et al. 2013; Monterrosso et al. 2014; Hua et al. 2020). Nevertheless, despite this night-time preference, we would describe these carnivores in two categories from their behavioral activities found. The leopard would be qualified as a "cathemeral species" as it shared activity between daytime and night-time and mesocarnivores qualified as "nocturnal preferred".

Contrary to the first hypothesis, these carnivores did not reveal significant changes in site occupancy across years, a fact evidenced by the rate of change in occupancy as a noticeable rise was documented from IS_1 to IS_2. This rate demonstrated stability in both IS (Table 2) for non-native species, yet for human, the occupancy markedly changes alternately. The recent Natural Forests Protection Program (NFPP) policies of the China national government for habitat restoration and improvement of management strategies within the TPNR would be responsible for constant carnivores estimates (Vitekere et al. 2020b; Zhu et al. 2021). These NFPP measures have enlarged the size and enhanced the forest quality of the PA (Xu et al. 2009; Wei et al. 2014). Furthermore, the homogeneousness effects due to the landscape features (case of the TPNR ecosystem) can also explain the native carnivores' site occupation, as found by Kass et al. (2020). The PA's outside intense disturbances would promote a type of lockdown for wildlife in the TPNR.

Regarding human occupancy in a PAs, findings opposite to ours were established by Farris et al. (2017), where this occupancy progressively increased over five years. Yet the same results revealed an alternate frequency of a lesser rising and diminution of dog occupancy over time. For

our study, both non-native and native carnivore species were well detected (except the dog, but with normal detectability ≥ 0.20). The estimated detection values determine the occupancy veracity, particularly when sampling sites and incidences are small (Royle and Nichols 2003; MacKenzie et al. 2006). Therefore, when species are well detected within their habitat (detection probability ≥ 0.30 for repetitive sampling occasion ≥ 5), the occupancy estimates would not be considered biased (Nicholson and van Manen 2009). As these changes in species' site occupation were weaker than expected, it is perhaps worth exploring disturbances, biophysical and environmental variables effects. Nonetheless, although the insignificant gap between both non-native and native carnivore species' occupancy equilibrium (except dog), carnivores were characterised by low occupancy equilibrium values than non-native species. Thus, it is evident that as long as native carnivores depict low occupancy equilibrium compared with non-native species within the TPNR, their long-term existence is substantially threatened since non-native species are potential sources of danger for PAs management worldwide.

Spatiotemporal Overlap Patterns

In the co-occupation framework, the pairwise human-carnivores portrayed a general trend of indirect space overlap with all carnivore species referring to the SIF estimates and contrary to our hypothesis. The leopard was the most influenced carnivore by human presence (all SIF > 1) as this species (leopard) was at equilibrium for night and daytime, inducing a high time overlap with non-native species (all $\Delta_4 \geq 0.73$). Our findings revealed that, spatially, the leopard did not avoid zones with human presence as previously found with other top predators (*e.g.*, Flores-Morales et al. 2019 for the Coyote *Canis latrans*, Guerisoli et al. 2019 for Puma *Puma concolor*, and Mori et al. 2020 for Wolf *Canis lupus*). Yet, Zhu et al. (2021) found that anthropogenic disturbances affect leopard's density in this area. However, leopard's activities were generally nocturnal, and specifically crepuscular; logically in the TPNR, the leopard may avoid contact with non-native species, specifically human, concentrating its activity bouts late in the dusk hours to avoid harmful contacts. On the other hand, the leopard cat and fox depicted a high SIF with human than the leopard did with human. Indeed, species differ in their aptitude to adapt to human presence on their degree of specialization in habitat use and ranging habits (Carricondo-Sanchez 2018). Some species can shift and create an adaptation to human presence due to their ecological behavior. Although there was a reduction of detectability of the leopard in the site where human was signaled ($r^{BA} < r^{Ba}$), the human presence had no substantial effect on leopard site use (Table 3A compared to Fig. 3). Leopard site occupation was even higher in the SP_2 in sites where leopards initially occupied the area; given that humans were also present (ψ^{BA}, Table 3A). Other studies have documented this fact

(Carter et al. 2015; Farris et al. 2017) and corroborated our findings. In a PA with anthropogenic activities, human site occupation has always been followed with disturbance effects on the site, attracting small and average bodied-size mammals. These zones in PAs would be in the vicinity of boundary areas where PA managers lack the authority, resources, and funding to establish wildlife management regulations (Lindenmayer et al. 2012; Bauer et al. 2015). Therefore, the fox is a potential species to be attracted there. Thus, this carnivore presence would be perceived as colonisation rate since it is reflected as a conditional occupancy (MacKenzie et al. 2006). The colonisation also did not greatly fluctuate with human presence and human absence in the site. In our investigation, the growth in human-carnivores spatiotemporal co-occurrence over these three years is a measure of human invasion related to a wide range of anthropogenic activities as resource extraction and livestock pasture.

The leopard showed direct interactions within the site co-occupation with livestock (all SIF > 1). At the same time, the leopard cat and the fox were characterised by independent interactions (SIF close to 1), with the exception of the leopard cat in SP_1. Also, the temporal overlap between the leopard and livestock was apparent ($\Delta_4 = 0.75$) and can be elucidated by previous findings in the TPNR since the leopard feeds regularly on livestock (Consolee et al. 2020; Vitekere et al. 2020a), our results found even leopard with a higher occupancy in livestock presence. Such co-occurrence has been seen by Lovari et al. (2015) in an analysis of common leopard and livestock coexistence in an area of Nepal. Other similar studies stated that livestock had been revealed as the second important prey of the top predators (Okello et al. 2014; Ciucci et al. 2018). Livestock becomes a central component of the prey of leopards probably because there is a lack of defence by herds' keepers, particularly during the calving period inside the PAs. These findings are partially in accordance with the temporal hypothesis given that livestock and leopard use the same time and overlap leads to predation. Nevertheless, when farmers undertake their livestock defence they habitually use retaliatory procedures to harm predators (Treves and Karanth 2003; Cromsigt et al. 2013). The TPNR landscape is reputed to host more farmers, revealing that within this landscape livestock is more present and carnivore avoidance interactions are more unlikely to occur. So, direct interactions of leopard with livestock in the TPNR indirectly launches an interaction between humans and carnivores, which always end in human-carnivore conflict (Consolee et al. 2020; Vitekere et al. 2020a). Occasionally fences are built and have proven palliative solutions to impede livestock encroachment from PAs (Lovegrove et al. 2002).

In an area characterised by limited resources due to its uniformity of habitats, it is common to observe native species being destabilised by non-native species. The heterogeneity of a landscape is somewhat responsible for ecological niche diversification (Eppstein et al. 2006; Soto and Palomares 2015), and trails have a significant role in the invasion of PAs. This is the case of the TPNR, which

is crossed by diverse trails. A strong and positive correlation between trails and dog presence in PAs was mostly documented when studying non-native species effects in an ecosystem (Farris et al. 2016; Farris et al. 2017). The dog was characterized by higher spatiotemporal overlaps with leopards (all SIF > 1 except in SP_1, and $\Delta_4 = 0.74$). A significant spatial overlap was depicted by the apparent co-occurrence between the dog and fox in all SP with the fox. While this invasive species and the fox are similar in body size, they are not ecologically similar, and the principle of competitive exclusion (MacArthur and Levins 1967) may not be applied. Many studies brought out the fox preference for human-disturbed habitat (Macdonald et al. 2004; Hughes and Macdonald 2013; Barull et al. 2014; Mori et al. 2015; Vitekere et al. 2020b). The dog being at occupancy equilibrium in our study supports obvious inferences about its long-term presence in the TPNR. In a Madagascar study, Farris et al. (2016) found the dog excluding native carnivores in some areas within his study area. Free-ranging domestic dogs are amongst the most well-known worldwide non-native species that often affect native carnivores. This situation is a little challenging when there is a spatiotemporal overlap with native carnivores. Being also a carnivore, the dog will interact with native carnivores by becoming a real competitor (Hughes and Macdonald 2013; Vanak et al. 2013; Mella-Méndez et al. 2019). It can reduce the prey biomass (Frank et al. 2014; Wierzbowska et al. 2016), transmit disease (Rasambainarivo et al. 2017; Mella-Méndez et al. 2019) and undertake direct intra-guild aggression in PAs (Hughes and Macdonald 2013). Our study displays the dog's ability to influence the temporal patterns of native carnivores. Precisely, we add the evidence to the body of literature the competitive dynamics between the dog and the leopard within a human-dominated landscape.

However, while mesocarnivores were strongly bounded to the night-time, they exhibited some plasticity within this preferred temporal interval as their Δ_4 were low than 0.75. Indeed, none of these two species (leopard cat and fox) displayed a constant activity pattern in nocturnal times. Further researchers have found the wild cat and fox using night-time but with some evident activities shifted in the diurnal period (Barull et al. 2014; Monterosso et al. 2014); consequently, Monterosso et al. (2014) qualified them as "facultative nocturnal". According to our findings, we assumed that, regardless of the high night-time rate of activities, these mesocarnivores tried to avoid the overlap activities with the big feline (leopard) to maximize their ability in the landscape and moderate the risks for antagonistic overlap. Yet, this fact does not necessarily mean they avoid leopard, because the nocturnality of some medium-sized carnivores is proved to coincide with their prey's activity. In contrast, with 31% of its diel activity in the daytime, the red fox did not totally avoid this period. Previous studies found the red fox using important daytime activity (Cavallini and Lovari 1994; Adkins and Stott 1998). Equivalent observation is also found for the leopard cat, which had 29% of our study's daytime activities, corroborating other studies that found 20–21%

(Germain et al. 2008; Monterosso et al. 2014). Generally, these two carnivores did not depict time overlap with non-native species, except at a small level, (20–30% only in the daytime) as all non-native species were characterized by a diel activity in daytime Δ_4 of pairwise species combination less than the 0.50. This fact would have some advantages in these two species' ecology, particularly allowing flexibility in their diel activity patterns (as both mesocarnivores depicted spatial overlap with non-native species). It can permit the facilitation of accessing other affordable prey in their habitat or support, avoiding the riskiest periods of the day for both non-native species and top predators. However, Mori et al. (2020) found that the red fox is amongst mesocarnivores that often overlap spatially and temporally with top predators. Yet, these findings were not completely corroborated by the STV for species pairings as the fox implied the average STV with non-native species (from 0.46 to 0.66). For the pairing species with highest STV (human-leopard, livestock-leopard, dog-leopard even dog-fox) this value reflects the state of spatiotemporal aggregation. Such scenario is the riskiest state for native species as it portrays potential threats for shared space and probably leads to more other possible vulnerabilities (negative interactions) to native species (Okello et al. 2014; Rasambainarivo et al. 2017; Mella-Méndez et al. 2019; Farris et al. 2020) since they occur in the same space at the same time.

CONCLUSIONS

Although the principal aim of PAs is to protect biodiversity, elusive species such as carnivores have always experienced interspecies threats that are hard to detect since carnivore studies often rely on passive sampling when investigating species' spatiotemporal threats (Farris et al. 2017; Farris et al. 2020). In this study, the presence of invasive species would be considered to be dependent on human presence. Only humans would be presumed to interact with wildlife directly, but livestock and dogs depicted obvious overlaps with carnivores. Most livestock interactions with mesocarnivores were indirect, but the dog influenced the leopard and the fox' site occupation more.

For the conservation implications, our results suggest that the presence of wild prey could reduce livestock depredation by the leopard and thus reduce the spatiotemporal overlap between carnivores and livestock. This would help to facilitate coexistence patterns with humans within the TNR and imply sustainable management of the reserve's landscape by reducing retaliatory measures. Such outcomes could be used to develop targeted education programs that inform local people living inside and outside the TNR or travelling with domestic dogs in the PA, on the negative impacts their dogs may have on native carnivores. Considering spatiotemporal patterns

using two niche dimensions can potentially lead to confusion in inferences interactions. For example, one might conclude that a native species has been impacted by non-native species when the two species do not demonstrate any temporal overlap because they use different time activities. Therefore, studies integrating landscape features (disturbances, habitat type, and diet or prey) are necessary to understand better these intrinsic interactions in species, which are essential drivers of population and community dynamics over time in Protected Areas.

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