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## Range-wide camera traps reveal potential prey species for Javan leopards

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## ABSTRACT

Prey depletion poses a threat to large carnivores worldwide. The Javan leopard (*Panthera pardus melas*), the last remaining apex predator on the Indonesian island of Java, is facing numerous threats from human activities including poaching, habitat loss and prey depletion. Despite the fact that the Javan leopard is an adaptable and opportunistic predator capable of surviving in various environments, our understanding of its prey and predator-prey interactions is still limited, which is crucial for their conservation. Using camera trap data collected from four national parks (i.e., Ujung Kulon, Gunung Gede Pangrango, Meru Betiri, Alas Purwo) that represent four distinct terrestrial ecoregions across the island of Java, we investigated the species richness, relative abundance, and spatial-temporal overlap in activity patterns between the Javan leopard and other animals that coexist in the same location. Our analysis of 7461 independent photos, covering 12,983 camera trap days, revealed that areas with the presence of Javan leopards exhibited higher species richness and abundance compared to those without the presence of Javan leopards. In addition, we found that the activities of banteng (*Bos javanicus*), barking deer (*Muntiacus muntjak*), Javan deer (*Rusa timorensis*), Javan mousedeer (*Tragulus javanicus*), wild boar (*Sus scrofa*), junglefowl (*Gallus spp.*), spangled ebony langur (*Trachypithecus auratus*), Javan rhino (*Rhinoceros sondaicus*), long-tailed macaque (*Macaca fascicularis*) and dhole (*Cuon alpinus*) were highly overlapping with those of Javan leopards in space and time, suggesting that these species are potential candidate prey for Javan leopards. To our knowledge, this is the first comprehensive investigation of potential prey for the Javan leopard that utilizes camera traps from all four types of terrestrial ecoregions on Java Island. The findings of this study may serve as essential information for the conservation of this critically endangered species.

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## 1. Introduction

The Javan leopard (*Panthera pardus melas*), the last remaining apex predator on the Indonesian island of Java, is threatened by poaching, habitat loss, and prey depletion, like many other large carnivores worldwide (Carbone et al., 2011; Karanth and Chellam, 2009; Wibisono et al., 2018; Woodroffe, 2000). Availability of a healthy prey base throughout their habitat range is crucial for the long-term survival of these top predators (Lovari and Mishra, 2016; Creel et al., 2018). When there is insufficient prey, the population of large carnivores may decline and potentially become locally extinct (Wolf and Ripple, 2016). The importance of both abundance and diversity of prey for large carnivores has been highlighted by many studies. For instance, mountain lions (*Puma concolor*) kill a high diversity of species to ensure their survival in the Santa Cruz Mountains of California (Smith et al., 2016). A reduction in large ungulate prey has led to the decline of tigers (*Panthera tigris*) in southern India (Ramakrishnan et al., 1999). In the Serengeti ecosystem, the abundance of large carnivores in an area is directly connected to the variety of prey available for predators (Sinclair et al., 2003).

Large carnivores are usually found in areas with a rich and diverse prey species (Tshabalala et al., 2021). Thus, large carnivores are often considered as flagship or umbrella species to promote biodiversity conservation (Weber and Rabinowitz, 1996; Karanth and Chellam, 2009; Caro, 2010). For example, it has been found that there is a strong positive correlation between the presence of large carnivores and the diversity of prey (Berger et al., 2001; Sergio et al., 2004; Ripple and Beschta, 2006). Some studies indicate that the presence of large and medium-sized carnivores such as the tiger (*Panthera tigris*), clouded leopard (*Neofelis nebulosa*), dhole (*Cuon alpinus*), and Tibetan fox (*Vulpes ferrilata*) is responsible for the greater variety of mammals in protected areas than in non-protected areas (Dorji et al., 2019). The connection between carnivores and their prey is not only visible in variety, but also in abundance (Rich et al., 2017). The abundance of prey enables carnivores to delineate territories and reduces the energy expended on hunting, thereby improving the overall fitness and reproductive success of their populations (Balme et al., 2007; Winterbach et al., 2014). For instance, in the Faragosa-Fura landscape of the Southern Rift Valley, Ethiopia, spotted hyenas (*Crocuta crocuta*) prefer areas with abundant medium-sized ungulates (Gebo et al., 2022). Similarly, leopards (*Panthera pardus*) in Karongwe Game Reserve, South Africa, show a tendency to reside in areas that have a higher abundance of prey (Owen, 2012).

The leopard's flexibility to consume a wide range of prey species and adapt to a variety of environments and climatic conditions contributes to its success as a generalist and opportunistic predator (Ario et al., 2018; Bothma and Walker, 1999; Santiapillai and Ramono, 1992). Despite its adaptability, the leopard is still vulnerable to threats of prey depletion (Jacobson et al., 2016; Traylor-Holzer et al., 2018; Ario et al., 2022). The low leopard population in South Luangwa National Park, Zambia, is attributed to prey depletion (Rosenblatt et al., 2016). In the Congo Basin rainforest, the decline in leopard populations has been associated with reduced prey availability caused by human bushmeat hunting (Henschel et al., 2011). In addition, prey availability has been found to impact the population density of leopards (Ngoprasert et al., 2007; Qi et al., 2015; Wibisono et al., 2018). Thus, maintaining adequate prey populations is the focus of leopard conservation efforts, as this is crucial for their survival (Farhadinia et al., 2018).

The Javan leopard typically hunts small to medium-sized mammals as its prey. Several studies have documented the diverse dietary habits of the Javan leopard. Previous studies have shown that the primary prey of the Javan leopard consists of species belonging to the Cervidae, such as barking deer (*Muntiacus muntjak*), Javan mousedeer (*Tragulus javanicus*), and Javan deer (*Rusa timorensis*), as well as species from the Suidae, such as wild boar (*Sus scrofa*) (Seidensticker et al., 1980; Santiapillai and Ramono, 1992; Ario et al., 2018). Some studies suggest that the long-tailed macaque (*Macaca fascicularis*), Javan langur (*Trachypitecus auratus*), Javan gibbon (*Hyllobates moloch*), and Javan surili (*Presbytis comata*) are also among the prey species targeted by Javan leopards (Seidensticker et al., 1980; Santiapillai and Ramono, 1992; Rizal and Imron, 2015). Apart from these species, it is believed that Javan leopards also prey on Asian palm civets (*Paradoxurus hermaphroditus*) and green peafowl (*Pavo muticus*) (Seidensticker et al., 1980; Gunawan, 2010). Despite the fact that the Javan leopard is an adaptable and opportunistic predator capable of surviving in various environments, our understanding of its prey and predator-prey interactions is still limited.

Common methods for determining the prey species of large carnivores involve a combination of field observations and fecal DNA analysis (Symondson, 2002; Boitani and Powell, 2012; Mumma et al., 2014; Martínez-Gutiérrez et al., 2015). However, obtaining accurate data on the diets of large carnivores, particularly in rare or elusive species like Javan leopards, is often challenging through direct field observations and expensive fecal DNA analysis (Thompson, 2004). Camera trapping is a reliable, cost-effective, and non-invasive technique for collecting data on wildlife species, which can help identify potential prey species for large carnivores (Khorozyan et al., 2008; Smith et al., 2020; Palmer et al., 2022; Gelmi-Candusso et al., 2023). It enables researchers to minimize any disturbances in the behavior of the species under study (O'Connell et al., 2011). Camera trapping has been used to create faunal checklists, detect elusive or endangered species, and estimate the abundance of species (Rovero et al., 2013). Several camera trapping studies have been conducted on the Javan leopard, focusing on various aspects such as carnivore density, spatiotemporal interaction between predator and prey, and identification of potential prey species (Rustiadi and Prihatini, 2015; Rahman et al., 2018; Pudyatmoko, 2019; Ario et al., 2022). However, these studies were executed either on a local scale or at the individual national park level. Until recently, a comprehensive island-wide analysis of camera trap data has not yet been conducted to identify the potential prey for the Javan leopard.

In this study, we aim to identify potential prey species for Javan leopards by utilizing camera trap data from four national parks that represent the four ecoregions throughout Java Island. Specifically, we set out to: (1) compare the animal species richness in areas with and without the presence of the Javan leopard; (2) determine whether the Javan leopard prefers the areas with a relatively high abundance of coexisting animal species; and (3) investigate the spatiotemporal overlap in activity patterns between the Javan leopard and other animal species that coexist in the same location, and thus identify potential prey species for the Javan leopard.

## 2. Materials and methods

### 2.1. Study area

Java is Indonesia's most densely populated island that has a land area of 129,442 km<sup>2</sup> and is home to 145.1 million people, or 57 % of the Indonesian population (Statistics Indonesia, 2020). It has a tropical climate with annual mean air temperatures between 26.4°C and 29.6°C with an average humidity of 75 %. West Java is more humid than East Java, and mountainous regions receive significantly more precipitation. The highlands of West Java receive more than 4000 mm of annual precipitation, while the north coast of East Java receives only 900 mm annually (Whitten et al., 1996; Dsikowitzky et al., 2018). We identified four national parks, i.e., Ujung Kulon National Park (UKNP), Gunung Gede Pangrango National Park (GGPNP), Meru Betiri National Park (MBNP), and Alas Purwo National Park (APNP) and used them to represent four distinct ecoregions on Java (Olson et al., 2001) (Fig. 1). UKNP, GGPNP, and APNP denote the Western Java rainforests, Western Java montane rainforests, and Eastern Java-Bali rainforests, respectively. Furthermore, the MBNP encompasses the Eastern Java-Bali montane rainforests in its northeastern region, while the remaining areas of the park are Eastern Java-Bali rainforests. The characteristics of these four national parks are presented in Table 1.

### 2.2. Camera trap data

A total of 201 infrared camera traps deployed in four national parks known to have Javan leopards over a range of second-half-year periods (i.e., June to December) spanning from 2020 to 2022 were used in this study (Fig. 2). Each camera station is considered one sampling unit that covers an area of 1 km<sup>2</sup>. The specific locations of these camera traps were primarily selected based on known pathways frequented by animals and proximity to water sources. To reduce the spatial inter-dependence between camera stations, we selected the camera traps that were positioned at a distance of > 1 km (Moreira-Arce et al., 2015; Pudiyatmoko, 2019). The camera traps were securely attached to the trees at a height that ranges between 30 and 50 cm above the ground, without using any bait to lure the animals. The infrared cameras were active 24 hours per day. They switched to photo mode to capture one image, with a 3-second interval between each image. The statistics of the camera trap effort in the four national parks are presented in Table 2.

To avoid bias in small animal identification and prioritize common prey species for the Javan leopard, we shortlisted photos of animal species, specifically those that are equal to or larger than the Javan mousedeer (*Tragulus javanicus*), with a body length of 45 cm, a body height of 30 cm, and a weight of 2 kg (Matsubayashi et al., 2003). Initially, we eliminated images depicting humans, empty images devoid of objects, and unidentified images. We then compiled a comprehensive inventory and conducted a quantitative analysis to determine the total count of species captured by each camera trap. We also calculated naïve occupancy (i.e., proportion of camera traps to detect species) for every species to ensure that we selected target species with sufficient images for subsequent analysis (Rovero and Zimmermann, 2016). To ensure the ability to yield sufficient captured images, we adopted a threshold of 0.1 for naïve occupancy as proposed by MacKenzie et al. (2004).

### 2.3. Calculation of species richness

Species richness is a straightforward and essential measure of biodiversity that is widely used in ecological research (Fleishman et al., 2006). The simplest way to calculate species richness is by counting the number of different species in a given area. To calculate the species richness, we first separated the camera trap stations that captured images of Javan leopards from those that did not capture images of Javan leopards. Subsequently, we quantified the number of species present in each camera trap station. We then compared the number of species (species richness) between two distinct conditions: the camera traps that successfully captured Javan leopards

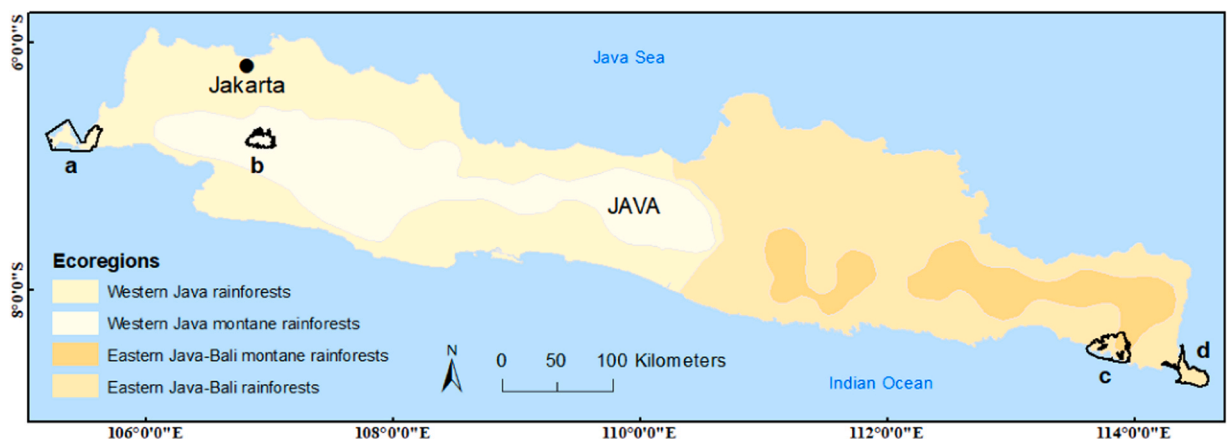
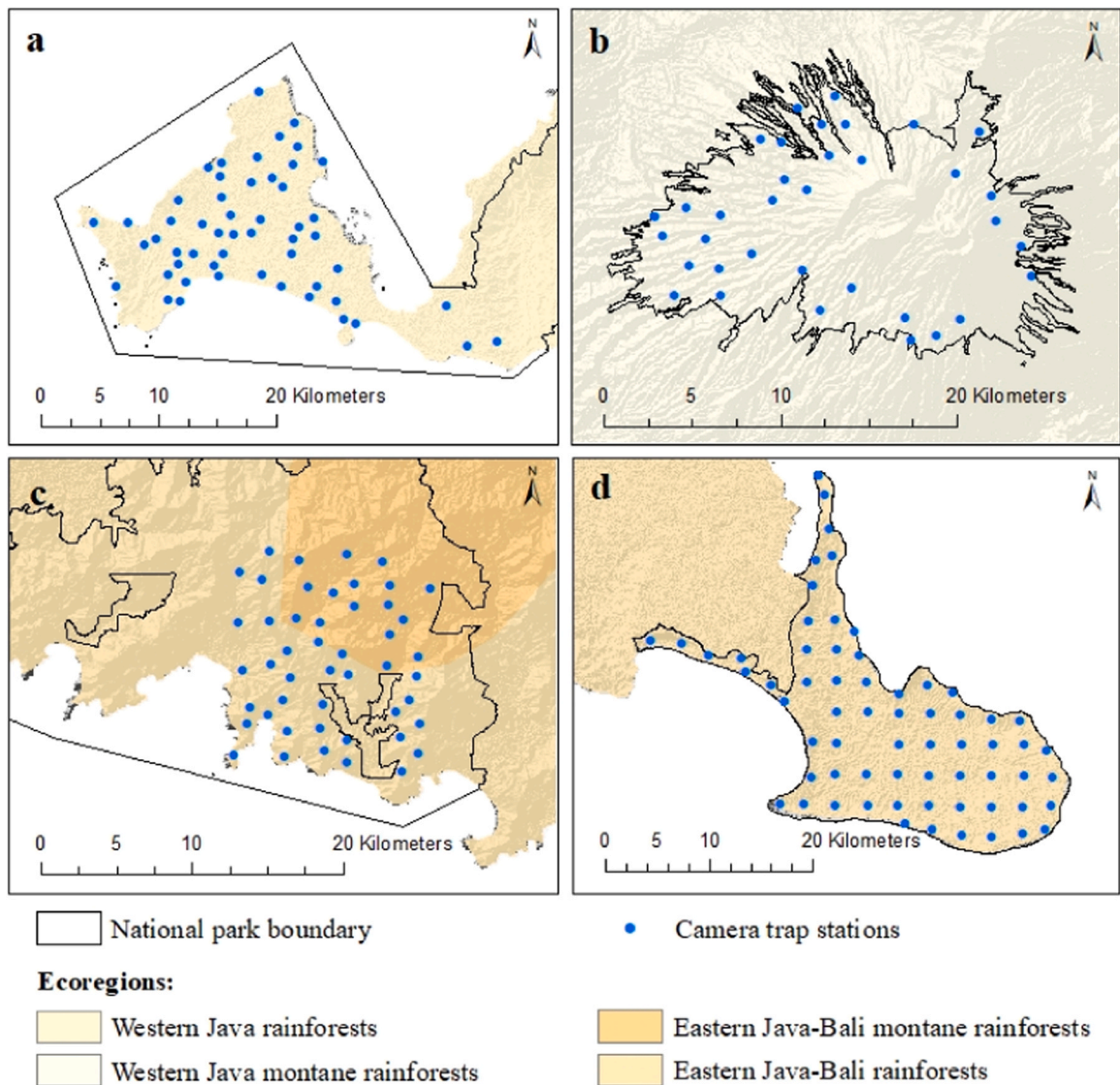


Fig. 1. The location of the four national parks representing the four distinct terrestrial ecoregions on Java Island used in this study: (a) Ujung Kulon National Park, (b) Gunung Gede Pangrango National Park, (c) Meru Betiri National Park, (d) Alas Purwo National Park.

**Table 1**

Characteristics of the four national parks used in this study: Ujung Kulon National Park (UKNP), Gunung Gede Pangrango National Park (GGPNP), Meru Betiri National Park (MBNP), Alas Purwo National Park (APNP).

	UKNP	GGPNP	MBNP	APNP
Ecoregion	Western Java rainforests	Western Java-Bali montane rainforests	1. Eastern Java-Bali montane rainforests 2. Eastern Java-Bali rainforests	Eastern Java-Bali rainforests
Size (hectare)	58,618	24,271	52,626	44,037
Elevation (m)	0 – 620	500 – 3019	0 – 1223	0 – 322
Wet season	October to April	October to April	November to March	November to April
Dry season	May to September	May to September	April to October	May to October
Temperature (°C)	25 – 30	20 – 30	25 – 31	26 – 28
Rainfall (mm/year)	3200 – 3300	3000 – 4200	1200 – 2800	1100 – 1500
Humidity (%)	80 – 90	80	60 – 70	75 – 81



**Fig. 2.** The distribution of camera trap stations in the four national parks: (a) Ujung Kulon National Park, (b) Gunung Gede Pangrango National Park, (c) Meru Betiri National Park, (d) Alas Purwo National Park.

**Table 2**

Summary statistics of the camera-trap sampling effort in the four national parks: Ujung Kulon National Park (UKNP), Gunung Gede Pangrango National Park (GGPNP), Meru Betiri National Park (MBNP), Alas Purwo National Park (APNP).

	UKNP	GGPNP	MBNP	APNP	Total
Camera stations	53	35	48	65	201
Survey period	Jun – Sep 2022	Jun – Sep 2021	Sep – Nov 2020	Sep – Dec 2022	
Average days	79 ± 21	67 ± 24	46 ± 10	65 ± 13	
Effective trap night	4200	2349	2207	4227	12,983
Identified photos	4929	652	3133	3625	12,339
Independent photos	2693	352	1585	2831	7461
Camera captured leopard	32	24	27	15	98
Camera not captured leopard	21	11	21	50	103

and those that did not.

#### 2.4. Calculation of species relative abundance

Camera trap data cannot directly provide accurate estimates of species abundance due to detection variability, non-uniform detection rates, and capture and recapture issues (O'Connell et al., 2011). To address these challenges, researchers often use the Relative Abundance Index (RAI) as an alternative measure when working with camera trap data (Liu et al., 2020; Tanwar et al., 2021). The RAI provides an estimate of the relative abundance of species based on the number of detections per unit of effort (e.g., per camera trap night). It is calculated using the average camera-trapping rate, which is the ratio of the total number of independent captures to the total number of trap nights. In this study, we calculated the RAI for each species to estimate their abundance. We used a 30 min interval to determine independent photo-capture events. Successive photo-captures of the same species taken less than 30 min apart were considered one event. The formula to calculate RAI is:

$$RAI = \frac{IP}{CTD} \times 100; \quad (1)$$

where *IP* is the total of independent photos of species, and *CTD* is the camera trap's active days. It then was scaled with 100-day traps (O'Brien et al., 2003; Rovero and Zimmermann, 2016).

#### 2.5. Spatial overlap analysis

To assess spatial overlap between the target species and the Javan leopard, we first applied a single-species occupancy model for each species. Then, we used the top occupancy model of each species paired with the Javan leopard occupancy (i.e., using two-species occupancy model) to evaluate their coexisting value (Burnham and Anderson, 2002).

##### 2.5.1. Single-species occupancy models

To model individual species occupancy, we applied the single-season occupancy function (R package 'wiqid' version 0.3.3). This function estimates species occupancy based on the recorded data of detection/non-detection for a single season, which incorporates site covariates and survey covariates. This modelling approach allows for the estimation of the occupancy ( $\psi$ ) and detection ( $p$ ) probability (Meredith, 2022). Occupancy refers to the probability of a particular species being present within a surveyed area. The detection rate denotes the likelihood of obtaining photographic proof of the species' existence when it is actually present. To construct the detection history, we used 14-day records constitute an "occasion" based on previous research for carnivores on Sumatra Island (Haidir et al., 2018; Widodo et al., 2022). The detection of species is denoted by 1, while non-detection is denoted by 0 (Linkie et al., 2007).

Site conditions have a significant impact on the occupancy of species. Therefore, we incorporated habitat attributes that play a crucial role in determining their distribution. The site covariates utilized in our study included elevation (McCain and Grytnes, 2010) and distance to rivers (Rich et al., 2016) as key variables describing the biophysical environment, while distance to the roads, distance to the settlements and distance to cultivated areas served as a measure of human disturbance (Linkie et al., 2007; Laurence et al., 2008; Wibisono et al., 2018). These covariates were acquired from the Indonesia base map (BIG, 2023). The elevation measurement for each camera trap was acquired by extracting the national digital elevation model. The distances to the river, road, settlement, and cultivated areas were calculated using the Euclidean distance method. The analyzes were performed using ArcGIS 10.8.2 software (ESRI, 2022). To avoid multicollinearity, we calculated the variance inflation factor (VIF). We excluded the variable with the highest VIF, then repeated the procedure until no variables had a VIF greater than 5 (Akinwande et al., 2015; O'Brien, 2007). We excluded the variables for distances to settlement and distance to cultivated areas from our occupancy model. The final predictor variables used in our models included elevation, distance to rivers and distance to roads. Furthermore, the survey covariate utilized in this study was the measure of effort, represented by the number of camera active days.

To determine the value of occupancy probability, we initially fitted occupancy models for each species by combining site and survey covariates. The models were chosen based on the AICc score, a corrected version of Akaike's information criterion. The top models that satisfied the criterion of having a  $\Delta AICc \leq 2$  and a model weight  $> 0.1$  were chosen due to their superior overall fit and

relative simplicity (Anderson and Burnham, 2002; Schuette et al., 2013; Rovero and Zimmermann, 2016). Finally, we calculated the mean of the top models to derive the ultimate values for occupancy probability for each species.

### 2.5.2. Two-species occupancy models

To analyze spatial overlap between individual target species and the Javan leopard, we applied single-season two-species occupancy estimation in R package 'wiqid' version 0.3.3 (Meredith, 2022). We conducted a paired analysis between each target species and the Javan leopard using the covariates from their respective top models. To fit the model of two-species occupancy, we assumed the Javan leopard to be the subordinate species (B) and other species as a dominant species (A) because the Javan leopard is affected by the existence of other animals, which are likely to be its prey (Karanth et al., 2017; Widodo et al., 2022). We employed an identical procedure to single-season occupancy estimation to determine the best-supported model.

To assess co-occurrence between species, we calculated the species interaction factor (SIF;  $\Phi$ ) for each paired species and Javan leopard with the formula:

$$\Phi = \frac{\psi_A \cdot \psi_{BA}}{\psi_A(\psi_A \cdot \psi_{BA} + (1 - \psi_A)\psi_{Ba})}; \quad (2)$$

where  $\psi_A$  denotes the probability of species A being present,  $\psi_{BA}$  represents the probability of species B being present given the presence of species A, and  $\psi_{Ba}$  represents the probability of species B being present given the absence of species A. The value of 1 signifies that the occupancy of the two species is random. A SIF value  $< 1$  indicates a higher probability of species avoidance, while a SIF value  $> 1$  indicates a higher likelihood of co-occurrence between species B and A than expected (Richmond et al., 2010; Pudyatmoko, 2019).

### 2.6. Temporal overlap analysis of paired-species

To assess the daily activity pattern of pairwise species, we used Kernel density estimators (KDE) and measured the coefficient of overlap ( $\Delta$ ) using the R package 'overlap' v0.3.4. The range of  $\Delta$  spans from 0 to 1, denoting no overlap to complete overlap, respectively. We used  $\Delta_1$  for the small sample size ( $n < 50$ ) and  $\Delta_4$  for the large samples. To calculate confidence intervals with a 95 % confidence level, we applied 10,000 bootstrap samples (Meredith and Ridout, 2021; Smith et al., 2023).

Eventually, to visually represent the species that frequently interact with Javan leopards, as determined by the overlap of their spatial and temporal distributions, we created a quadrant plot displaying the potential prey species for Javan leopards. The quadrant plots were generated by employing a threshold of co-occurrence ( $SIF > 1$ ) for spatial overlap and the median  $\Delta$  value for temporal overlap. In the plot, Quadrant I represents the potential prey species due to the most commonly encountered with the Javan leopard. Species found in Quadrant III are likely to be rarely encountered due to low spatial and temporal overlap. On the other hand, Quadrant II and Quadrant IV suggest alternative prey species that were opportunistically encountered in terms of time or space (Allen et al.,

**Table 3**

A list of recorded animal species with their naïve occupancy, independent photos, and relative abundance index (RAI) in the four national parks: Ujung Kulon National Park (UKNP), Gunung Gede Pangrango National Park (GGPNP), Meru Betiri National Park (MBNP), Alas Purwo National Park (APNP).

Common names	Naïve occupancy				Independent photos				Relative abundance index			
	UKNP	GGPNP	MBNP	APNP	UKNP	GGPNP	MBNP	APNP	UKNP	GGPNP	MBNP	APNP
Asian palm civet	0.53	0.11	0.77	-	123	16	230	-	3.42	0.54	12.69	-
Banded linsang	0.04	0.20	-	0.02	2	13	-	3	0.06	0.45	-	0.06
Banteng	0.75	-	0.17	0.32	337	-	16	69	7.81	-	0.69	1.54
Barking deer	0.85	0.14	0.94	0.85	568	8	426	1192	12.86	0.28	20.26	27.88
Binturong*	-	0.03	-	-	-	1	-	-	-	0.04	-	-
Dhole	0.17	-	0.02	-	14	-	1	-	0.41	-	0.05	-
Green peafowl*	0.06	-	0.02	0.02	5	-	1	4	0.10	-	0.04	0.07
Javan deer	-	-	0.13	0.11	-	-	48	60	-	-	2.02	1.27
Javan ferret badger*	-	0.09	-	-	-	5	-	-	-	0.17	-	-
Javan leopard	0.60	0.69	0.56	0.23	85	63	63	27	2.13	3.29	3.09	0.67
Javan mongoose	0.09	0.69	-	0.08	5	128	-	5	0.22	5.08	-	0.10
Javan mousedeer	0.68	0.26	0.27	0.32	498	23	47	208	12.02	0.98	2.57	4.55
Javan rhino	0.25	-	-	-	32	-	-	-	0.77	-	-	-
Junglefowl	0.19	-	0.58	0.29	36	-	191	189	0.98	-	9.69	3.37
Leopard cat	0.09	0.31	0.40	0.12	7	31	49	11	0.18	1.92	2.78	0.26
Long-tailed macaque	-	0.03	0.65	0.34	-	2	250	275	-	0.10	12.15	5.49
Spangled ebony langur	0.02	-	0.15	0.06	1	-	7	14	0.03	-	0.31	0.30
Sunda pangolin*	-	0.03	0.08	0.02	-	1	4	1	-	0.03	0.21	0.02
Sunda porcupine	0.21	0.14	0.40	0.20	35	7	48	62	0.75	0.29	2.47	1.38
Sunda stink-badger	-	0.11	-	-	-	8	-	-	-	0.42	-	-
Wild boar	0.98	0.63	0.77	0.86	945	42	198	532	21.88	2.29	8.62	14.00
Yellow-throated marten	-	0.09	0.04	0.51	-	4	6	179	-	0.14	0.40	3.93

Note: The asterisk (\*) indicates the species that were excluded in further analyzes, and the dash (-) indicates no recorded animal species.

2021; Sehgal et al., 2022).

### 3. Results

#### 3.1. A summary of the animal species caught by camera traps

Table 3 shows the 22 animal species that were recorded by the camera traps, including Javan leopard (*Panthera pardus melas*), Asian palm civet (*Paradoxurus hermaphroditus*), banded linsang (*Prionodon linsang*), banteng (*Bos javanicus*), barking deer (*Muntiacus muntjak*), binturong (*Arctictis binturong*), dhole (*Cuon alpinus*), green peafowl (*Pavo muticus*), Javan deer (*Rusa timorensis*), Javan ferret badger (*Melogale orientalis*), Javan mongoose (*Herpestes javanicus*), Javan mousedeer (*Tragulus javanicus*), Javan rhino (*Rhinoceros sondaicus*), junglefowl (*Gallus spp.*), leopard cat (*Prionailurus bengalensis*), long-tailed macaque (*Macaca fascicularis*), spangled ebony langur (*Trachypithecus auratus*), Sunda pangolin (*Manis javanica*), Sunda porcupine (*Hystrix javanica*), Sunda stink-badger (*Mydaus javanensis*), wild boar (*Sus scrofa*), and yellow-throated marten (*Martes flavigula*). Among these 22 species, the species with a naïve occupancy < 0.1 were excluded from subsequent analyzes, including binturong (*Arctictis binturong*), green peafowl (*Pavo muticus*), Javan ferret badger (*Melogale orientalis*) and Sunda pangolin (*Manis javanica*) (Table 3).

#### 3.2. Species richness and relative abundance

Table 4 shows that areas where Javan leopards were present had a higher average prey species richness  $4.74 \pm 2.15$  than those without Javan leopards  $4.21 \pm 1.81$  (p-value = 0.013). For the MBNP, UKNP, and APNP areas, MBNP exhibited the highest species richness, with an average of 5.63 species. UKNP and APNP followed closely with species numbers of 5.25 and 4.87, respectively. However, in GGPNP, the situation was different, as areas inhabited by Javan leopards tend to have a low species richness with a value of 2.91.

There was also a positive relationship between the presence of Javan leopards and the abundance of other animal species that coexist in the same location in the respective areas. The relative abundance index (RAI) values of Asian palm civet and Javan mousedeer were significantly higher in areas where Javan leopards were present (p-values 0.008 and 0.001, respectively). Other animal species that exhibited higher RAI in areas where the Javan leopards were present including the banded linsang, banteng, barking deer, Javan deer, Javan rhino, junglefowl, and wild boar. On the other hand, the presence of Javan leopards had a lower RAI of Javan mongoose and throated marten (p-values 0.024 and 0.019, respectively). The dhole, green peafowl, leopard cat, long-tailed macaque, spangled ebony langur, Sunda porcupine, and Sunda stink-badger were found to be less abundant, but not significant (Table S1).

#### 3.3. Spatiotemporal overlap

##### 3.3.1. Single-species occupancy models

Fig. 3 shows the estimated occupancy probability for the Java leopard and other 17 animal species. It shows that barking deer, Javan mongoose and wild boar had the higher occupancy rates (0.75). On the contrary, the spangled ebony langur, Sunda stink-badger and Javan deer had lower occupancy rates, with values of 0.21, 0.13 and, 0.12 respectively. The remaining species exhibited moderate occupancy rates, ranging from 0.3 to 0.59.

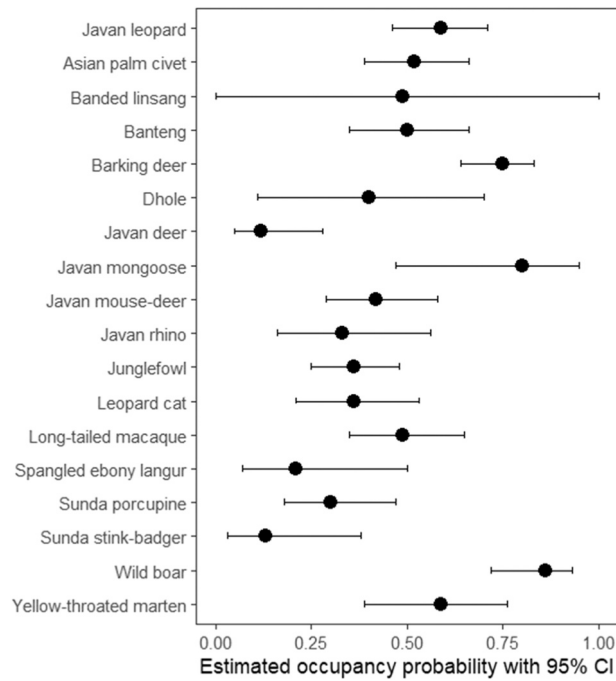
##### 3.3.2. Two-species occupancy models

Fig. 4 shows the spatial overlap between paired species with the Javan leopard. There was coexistence among all species that were paired with the Javan leopard, except for the Asian palm civet and banded linsang. Both species displayed avoidance behavior, as evidenced by their species interaction factor (SIF) values being less than 1 ( $\Phi = 0.99$  and  $\Phi = 0.81$ , respectively). The Javan leopard had a robust coexistence with three species: Javan mousedeer ( $\Phi = 1.35$ , 95 % CI: 1.13 – 1.77), Javan rhino ( $\Phi = 1.23$ , 95 % CI: 1.02 – 1.41), and junglefowl ( $\Phi = 1.33$ , 95 % CI: 1.07 – 1.72), as indicated by the 95 % CI not overlapping with 1. Other species observed in the area included banteng, barking deer, dhole, Javan deer, Javan mongoose, leopard cat, long-tailed macaque, spangled ebony langur, Sunda porcupine, wild boar, and yellow-throated marten had a range of SIF values between 1.05 and 1.62 (Table S2).

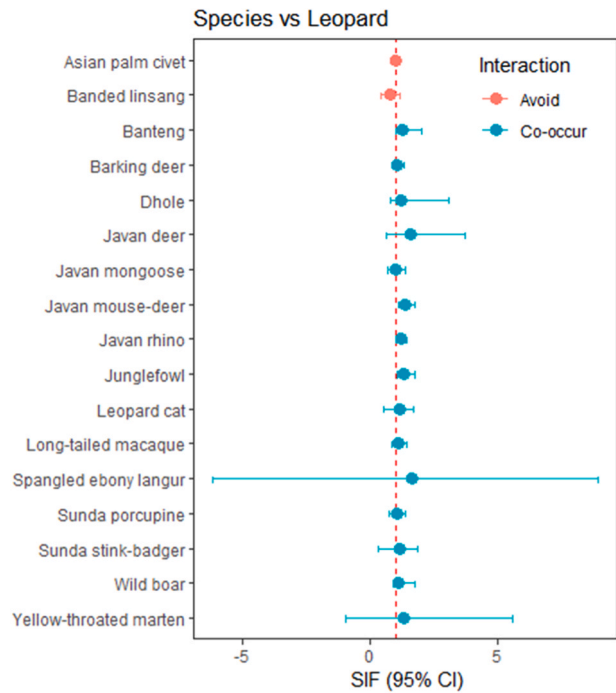
**Table 4**

Species richness in the presence and absence of the Javan leopard in the four national parks.

Study site	Species richness (mean $\pm$ SD)		p-value
	Presence	Absence	
Meru Betiri National Park	5.63 (2.10)	5.05 (1.63)	0.508
Ujung Kulon National Park	5.25 (2.08)	4.38 (1.12)	< 0.000
Alas Purwo National Park	4.87 (1.55)	4.04 (1.97)	< 0.000
Gunung Gede Pangrango National Park	2.91 (1.56)	3.00 (1.90)	0.079
Overall	4.74 (2.15)	4.21 (1.81)	0.013

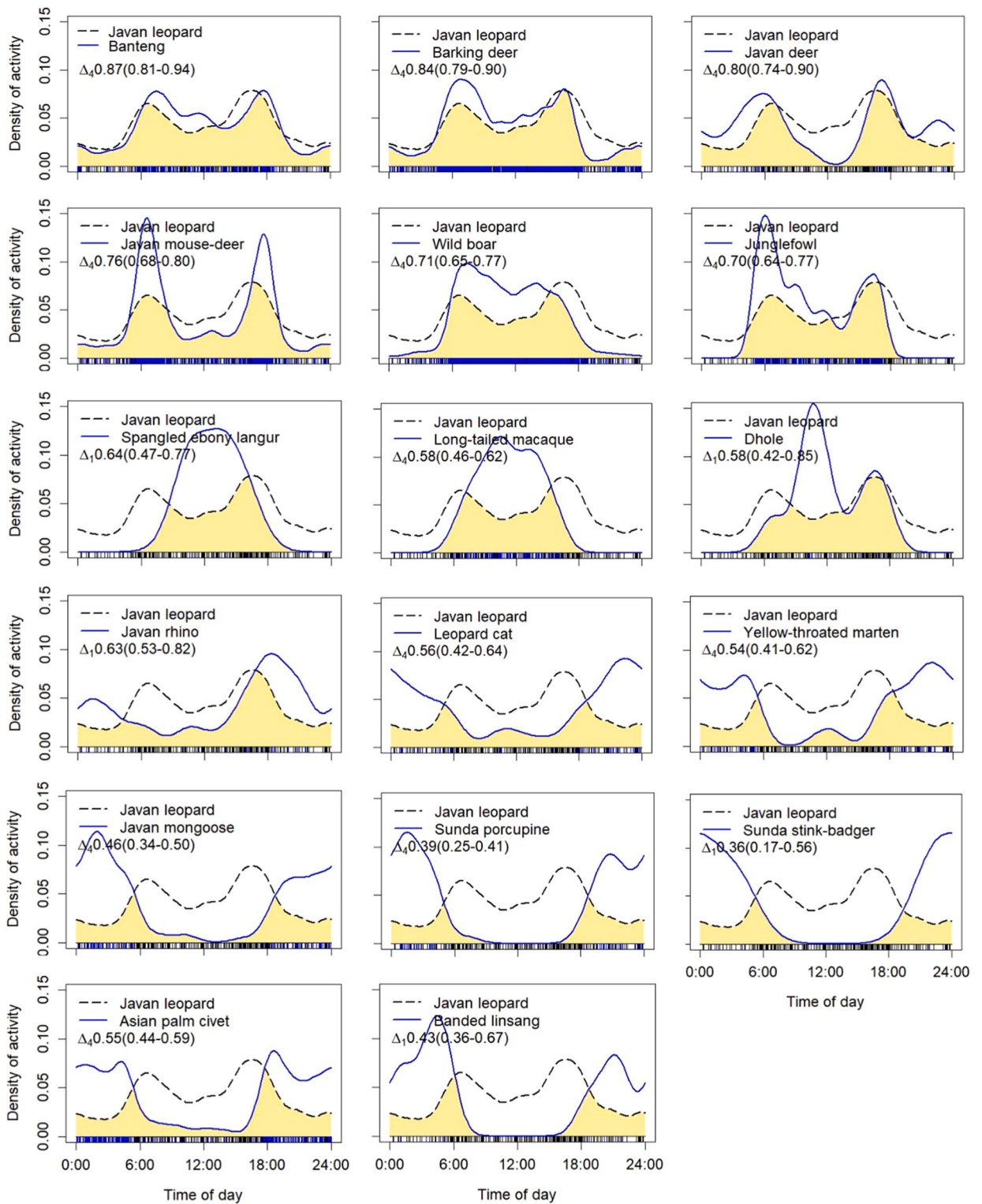


**Fig. 3.** The estimated occupancy probabilities for the Java leopard and other 17 animal species that coexist in the same location. These probabilities, along with their 95 % confidence intervals, are based on the average of models with  $\Delta AICc < 2$  and model weights  $> 0.1$ .



**Fig. 4.** Summary of spatial overlap indicated by species interaction factor (SIF) value ( $\Phi$ ) for paired species with the Javan leopard, with lower and upper confidence intervals of 95 %. The red dashed line represents the value of SIF equal to one. The value of SIF  $< 1$  indicates avoidance, SIF = 1 indicates random pattern, SIF  $> 1$  indicates co-occurrence.





**Fig. 5.** The estimation of daily activity pattern for targeted species versus the Javan leopard. The shaded light-yellow area indicates the temporal overlap. The estimated overlap is represented by  $\Delta$  with a 95 % confidence interval. The rug at the bottom of the plot represents the observations of activity time.

### 3.3.3. Temporal overlap of paired-species

Fig. 5 shows the temporal overlap between paired species with the Javan leopard. Among the coexist putative prey species, the analysis of activity pattern using Kernel density estimators (KDE) and the coefficient of overlap  $\Delta$  revealed that the banteng, barking deer and Javan deer exhibited the highest temporal overlap ( $\Delta > 0.80$ ), while the lowest overlap was observed in Javan mongoose, Sunda porcupine, Sunda-stink badger, yellow-throated marten and banded linsang ( $\Delta < 0.55$ ). The medium temporal overlap recorded in Javan mousedeer, wild boar, junglefowl, spangled ebony langur, long-tailed macaque, dhole, Javan rhino, and leopard cat Asian palm civet ( $0.55 \leq \Delta \leq 0.76$ ).

Fig. 6 illustrates the spatial and temporal overlap among the potential prey species. The species included in quadrant I were banteng, barking deer, Javan deer, Javan mousedeer, wild boar, junglefowl, spangled ebony langur, Javan rhino, long-tailed macaque, and dhole. No species were found in quadrant II, while quadrant III contained the Asian palm civet and banded linsang. Furthermore, quadrant IV included the leopard cat, yellow-throated marten, Javan mongoose, Sunda porcupine, and Sunda stink-badger.

## 4. Discussion

The Javan leopard plays a vital role in maintaining the structure and function of the ecosystem on Java island (Lindenmayer and Westgate, 2020; Wibisono et al., 2018). In this paper, we studied the species richness, relative abundance, and spatial-temporal overlap in activity patterns between the Javan leopard and other animals that coexist in the same location using camera trap data. We found that areas with the presence of Javan leopards exhibited higher species richness and abundance compared to those without the presence of Javan leopards. Furthermore, we found that the activities of banteng, barking deer, Javan deer, Javan mousedeer, wild boar, junglefowl, spangled ebony langur, Javan rhino, long-tailed macaque and dhole were highly overlapping with those of Javan leopards in space and time, suggesting that these ten species are potential candidate prey for Javan leopards. To our knowledge, this is the first comprehensive investigation of potential prey for the Javan leopard that utilizes camera traps from all four types of terrestrial ecoregions on Java Island.

Predators play a crucial role in shaping prey populations and community structure (Terborgh, 2015; Antiqueira et al., 2018). Large

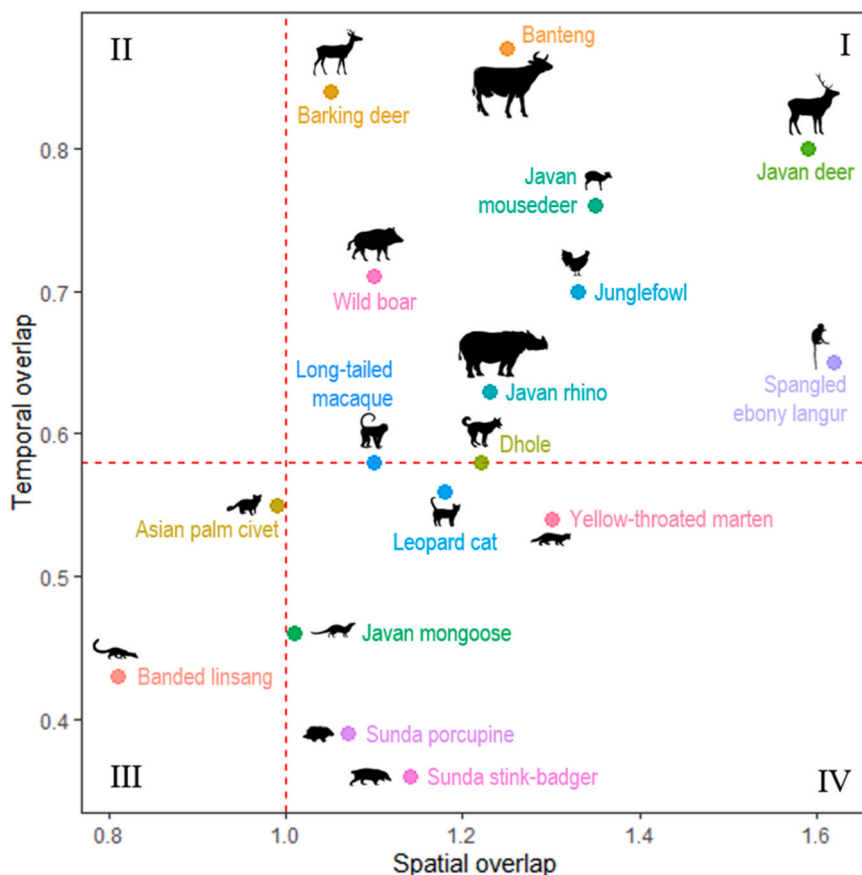


Fig. 6. Spatiotemporal overlap that indicates the potential prey for the Javan leopard. Quadrants of encountered species with the red vertical dashed lines indicate the spatial overlap threshold  $SIF > 1$  (co-occurrence), while the horizontal represents the median of temporal overlap ( $\Delta = 0.58$ ).

carnivores typically inhabit regions characterized by a diverse array of prey species (Tshabalala et al., 2021). Our study revealed that areas with the presence of Javan leopards tend to exhibit higher species richness than those without Javan leopards. This finding is in line with earlier research, which suggests that the presence of large carnivores has a strong positive correlation with the prey species richness (Berger et al., 2001; Sergio et al., 2004; Ripple and Beschta, 2006). However, a notable exception was observed in the Gunung Gede Pangrango National Park (GGPNP), where areas occupied by Javan leopards demonstrated lower species richness (Table 4). The area of GGPNP is narrow and surrounded by settlements and agricultural areas, making it vulnerable to anthropogenic disturbances (Ario et al., 2020). Such disturbances create significant pressure, forcing Javan leopards to live at higher elevations where species richness is commonly lower than at lower elevations (McCain and Grytnes, 2010). Consistent with the behavior of other carnivores, Javan leopards exhibit a preference for undisturbed forest habitats, avoiding areas where humans are active (Dias et al., 2019; Li et al., 2021). Consequently, Javan leopards are confined and compelled to adapt to the prevailing environment with limited prey in GGPNP.

We found that the Javan leopards preferred the areas with a relatively high abundance of animal species. This result agrees with Owen (2012), who stated that leopards tend to occupy areas with a higher prey abundance. Specifically, our study highlighted that among the observed animal species, Javan mousedeer, Javan deer, and wild boar were more abundant in areas with Javan leopards (Table S1). Predators may choose their feeding habitat based on prey abundance or alternatively where they are easier to catch (Hopcraft et al., 2005). Selecting the most abundant and easily accessible prey increases their chances of successful hunts to optimize energy expenditure and ensures their survival (Karanth and Sunquist, 1995). In contrast, it is notable that our findings showed a low abundance of Javan mongoose and yellow-throated marten in areas where Javan leopards were present. The low abundance of these small carnivores may be due to competition or predation by Javan leopards (Jarillo et al., 2020). This suggests that the interplay between Javan leopard and their prey, revealing how the abundance of prey plays a role in shaping the distribution and behavior of the predators in their natural environment.

We observed three clusters of potential candidate prey species based on the spatiotemporal overlap between the Javan leopard and other animals. The first cluster (quadrant I) includes species with high spatiotemporal overlap with the Javan leopard (Fig. 6). Within the first cluster, were identified three groups based on their frequency of mention in previous studies. The first group is the prey that have been confirmed by prior research comprises ungulates such as barking deer, Javan deer, Javan mousedeer, and wild boar, as well as primates, specifically the long-tailed macaque and spangled ebony langur (Seidensticker et al., 1980; Santiapillai and Ramono, 1992; Andheria et al., 2007; Ario, 2007; Ario et al., 2018; Gunawan et al., 2012;). Our findings indicated that ungulates and primates constitute potential candidate prey for Javan leopards (Fig. 6). This result aligns with previous studies. For instance, Hart et al. (1996) observed that leopards typically prefer medium-sized ungulates, which constitute over 50 percent of their diet, while primates account for approximately 25 percent. Moreover, Nakazawa (2020) and Seidensticker et al. (1980) have recognized primates as an important food source for leopards. Although prey preference can vary depending on the habitat condition, the prevalence of ungulates and primates (especially long-tailed macaques) in the Java forests (Hommel, 1987; Farida et al., 2006) suggests that they may serve as the primary prey for the Javan leopard. The second group is species rarely mentioned, including banteng and junglefowl (Gunawan et al., 2012; Rustiadi and Prihatini, 2015; Wahyudi et al., 2016). Our observations indicated that banteng is negatively affected by the presence of the predators. Instead, this large animal faced adverse effects from the presence of livestock, as Pudyatmoko (2017) reported in Baluran National Park. Although there is a lack of studies explicitly suggesting banteng as the Javan leopard's prey, there is evidence that the Javan leopard killed banteng in Ujung Kulon National Park (personal communication). In fact, banteng is the primary prey for leopards in eastern Cambodia and Thailand (Rostro-García et al., 2018; Simcharoen et al., 2008). Additionally, alongside the abundance of ungulates and primates, junglefowl emerges as another prevalent species in Java's forests (Compendio and Nishibori, 2021). Our research revealed a robust spatial overlap between junglefowl and Javan leopards (Fig. 4), indicating an increased likelihood of predation on this species by the Javan leopards. This result is in line with Rustiadi and Prihatini (2015), who identified junglefowl as potential prey for Javan leopards. Interestingly, similar observations have been made in Sanjay Gandhi National Park, India, where junglefowl are also considered potential prey for leopards (Edgaonkar and Chellam, 2002). This suggests that along with banteng, junglefowl can be an alternative prey for Javan leopards.

The third group is species never reported as prey for the Javan leopard consisting of Javan rhino and dhole. The spatiotemporal overlap between these two species and Javan leopards suggests that these animals may be hunted by Javan leopards. However, given its scarcity in the forest, it is unlikely that the Javan leopards actively prey on the Javan rhinos. Until recently, no evidence supports the claim that the Javan leopards' prey on Javan rhinos. Additionally, dholes and Javan leopards are sympatric species that share a preference for ungulates, such as bovids and cervids, as their diet (Nurvianto, 2018). Their coexistence is facilitated by temporal segregation and selective predation (Pudyatmoko, 2019). When hunting, dholes tend to target larger prey like banteng, as they are social predators (Karanth and Sunquist, 1995; Rahman et al., 2019). While there is no prior evidence of Javan leopards hunting dholes, their spatiotemporal overlap increases the likelihood of encountering each other, potentially leading to predation events.

The second cluster (quadrant IV) consists of species that coexist with the Javan leopard but demonstrated low temporal overlap (Fig. 6). This cluster includes the leopard cat, yellow-throated marten, Javan mongoose, Sunda porcupine, and Sunda stink-badger. Except for the yellow-throated marten, these species have been identified as secondary prey for the Javan leopard by Gunawan et al. (2012). Similarly, Hayward et al. (2006) reported instances of leopards consuming porcupines and mongooses. Additionally, exclusive information was obtained indicating a Javan leopard preying on a leopard cat in Meru Betiri National Park (personal communication).

The third cluster (quadrant III) encompasses species that actively avoid the Javan leopard in space and time (Fig. 6). It includes the Asian palm civet and banded linsang, which actively avoided the Javan leopard. Our findings differed from those of Gunawan et al. (2012), who suggested that these species serve as secondary prey for the Javan leopard. We suspect that the nocturnal behavior of these species may represent an adaptive strategy to evade predators, particularly Javan leopards (Fig. 5) (Creel et al., 2018). However, it is

worth noting that smaller nocturnal animals are known to be preyed upon by leopards in other regions, such as India (Andheria et al., 2007). This suggests that beyond the ten potential candidate prey species identified in our study, other species may still face the risk of predation by Javan leopards.

Our study identified ten potential candidate prey species for the Javan leopard using camera traps. However, comprehensively identifying prey species for the Javan leopard across various landscapes and ecosystems on Java island is challenging. This process is highly dependent on the choice of study sites, the number of study sites, the distribution of camera traps, and the survey period. In our study, only 201 camera traps were deployed in four national parks known to have Javan leopards. The data collected covered only the second half of each year from 2020 to 2022. The Javan leopards inhabit both protected and non-protected areas, indicating their ability to adapt and highlighting the need for broader conservation strategies (Gunawan et al., 2012; Wibisono et al., 2018). Additionally, wildlife occupancy fluctuates between dry and wet seasons, reflecting changes in prey availability and habitat conditions (Ario and Gunawan, 2016; Rahman et al., 2017). Due to the limitations in the number of study sites and the survey period, additional study sites with extended survey periods may be required to strengthen our findings.

## 5. Conservation implications

The use of camera trap data to analyze potential prey for the Javan leopard carries substantial implications for conservation endeavors. By identifying the prey species and understanding their richness and abundance, managers can develop targeted strategies to maintain and enhance these prey populations. This information is crucial for habitat management, specifically ensuring adequate food resources for leopards and preserving habitat features that benefit both predator and prey species. Additionally, the evidence from camera traps highlights the importance of the Javan leopard as a flagship species, aiding in mobilizing public and political support for conservation efforts. Incorporating these findings into local conservation strategies entails implementing measures such as potential prey monitoring, habitat restoration, anti-poaching initiatives, and community engagement programs. These measures will enhance the long-term sustainability of Javan leopards and their ecosystems.

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## CRedit authorship contribution statement

**Yohanes Wihariso:** Writing – review & editing, Data curation. **Asep Y. Firdaus:** Writing – review & editing, Data curation. **Febri A. Widodo:** Writing – review & editing. **Hariyo T. Wibisono:** Writing – review & editing. **Nur Kholiq:** Writing – review & editing, Data curation. **Wahyu Murdyatmaka:** Writing – review & editing, Data curation. **Andrew K. Skidmore:** Writing – review & editing, Supervision. **Tiejun Wang:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Andhika C. Ariyanto:** Writing – original draft, Visualization, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

The data that has been used is confidential.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e03020](https://doi.org/10.1016/j.gecco.2024.e03020).

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