Density and spatial partitioning of endangered sympatric Javan leopard (Felidae) and dholes (Canidae) in a tropical forest landscape

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Abstract. This study explores two large carnivores, Javan leopard (*Panthera pardus melas*) and dhole (*Cuon alpinus*) that are known to have an overlapping diet and are sympatric in the south-western part of West Java. We characterised their spatiotemporal habitat together with four medium-sized prey species. We used photographs collected along 39.420 night-traps from 108 camera-traps installed on the peninsula of Ujung Kulon National Park (UKNP). We are using maximum entropy modelling (MaxEnt) to investigate seasonal environmental factors. Concerning the dominant prey species, our results showed that distances to secondary forest edge were highly significant for both Javan leopard and dhole in wet and dry seasons. Javan leopard is mostly active at dawn and dusk, whereas spatially correlated with Javan mousedeer and red muntjac. Dhole exhibited diurnal activity and were avoiding Javan leopard to a certain extent. Its spatial use is overlapping with red muntjac, wild boar, and banteng. Using Spatially Explicit Capture-Recapture (SECR) methods, the density estimation for Javan leopard were 10.91 and 11.54 individuals/100 km^2 in wet and dry seasons, respectively. We confirmed UKNP as one of Indonesia's biodiversity hotspots and a critical area to preserve Javan leopard and dholes.

Key words: large mammals carnivores, primary prey, camera trap, SECR, MaxEnt, daily activity

Introduction

Over the last six decades, the debate on the role of ecological interactions and mechanisms depicting the coexistence of sympatric carnivore species (large felids and canids) continues. The interaction type is either sympatric species sharing the same space (Srivathsa et al. 2014, Karanth et al. 2017) or avoiding the resource-rich habitats because of the dominant competitor (Steinmetz et al. 2013, Swanson et al. 2014). Various approaches have been used to investigate the population size and partition of resources utilisation (Karanth & Nichols 1998, Efford 2004, Friedemann et al. 2016). Knowledge of the population size, distribution and spatiotemporal habitat use are important to evaluate population status, possible interactions among elusive predators, and to determine the management of conservation strategies (Potts et al. 2013, Rechetelo et al. 2016).

Javan leopard (*Panthera pardus melas*) and dhole (*Cuon alpinus*) are sympatric throughout the Javan leopards' habitat range. Both species received little conservation attention and locally compete with more charismatic species. Both Javan leopard and dhole experienced the same anthropogenic pressures and suffered a significant population decline. Javan leopard is listed in CITES Appendix I (2009) as an endemic critically endangered species to Java island (Ario et al. 2008, Stein et al. 2016). On the other hand,

dhole is widely distributed in South-East Asia. It is also listed as an endangered species in the IUCN Red List (Kamler et al. 2015). The range of both species is quite restricted and exist only in the protected areas at the eastern and western ends of Java Island (Ario et al. 2008).

Javan leopard and dholes represent appropriate subjects to study coexistence strategies. They are exploiting similar resources and significantly influencing the ecosystem structure. As predators, both species are controlling numbers of herbivores and reducing the pressure of grazing as well as browsing activities (Miller et al. 2001). Further, the elimination of large carnivores have the most significant anthropogenic impacts on nature (Estes et al. 2011). For examples the decrease of cougar (*Puma concolor*) densities induced higher densities of mule deer (*Odocoileus hemionus*) (Ripple & Beschta 2006) and poaching of lions (*Panthera leo*) that led to population explosion of olive baboons' (*Papio anubis*) conduce zoonosis intestinal parasites on humans (Estes et al. 2011).

Any trends in the information on population sizes and distributions are essential to the management of conservation. Still, no reliable estimation from any part of its range is available for both species. Currently, a combination method of camera trapping with non-spatial capture-recapture modelling (Karanth & Nichols 1998) and Spatially Explicit Capture-Recapture (SECR, Efford 2004) has been successfully used to estimate densities for nocturnal, elusive felids with distinct coat patterns. Hereinafter, studying distribution and habitat use for both predators and prey species to improve conservation strategies using spatial models has a become a common practice (McCullagh & Nelder 1989, Peterson et al. 1999, Robertson et al. 2001, Hirzel et al. 2002, Beaumont et al. 2005, Phillips et al. 2006). One of the most commonly used presence-only modelling for inferring species distribution, habitat use and environmental cues from occurrence data is the maximum entropy modelling (MaxEnt, Phillips et al. 2006). It allows users to fit models of varying complexity (Warren & Seifert 2011).

Camera traps which deliver full activity record data for 24 hours per day reveal the presence of cryptic and elusive animals in a particular habitat (e.g. Rahman et al. 2016). Here we reported the camera traps targeting rhinoceros in Ujung Kulon National Park (UKNP) Indonesia, accidentally providing the first insights into the estimation of population size and spatial interactions of Javan leopard and dhole in the protected rainforest. Through this study, we tend to provide the first density estimation for the Javan leopard by

SECR model. We also aimed to draw comparisons with the sympatric dholes by examining differences in habitat use and range in response to several physicals, biological, climatic and anthropogenic variables. Carnivores have been reported likely to adopt temporal, spatial, and spatiotemporal segregation as alternative mechanisms to facilitate sympatry by selecting the same habitat patches (Lovari et al. 2013, Karanth et al. 2017). We hypothesised at fine spatial scales, Javan leopard and dhole space patterns in UKNP might be overlapping. Furthermore, we also considered the possible use of spatial prey hypothesis, i.e. Java mousedeer (*Tragulus javanicus*), wild boar (*Sus scrofa*), red muntjac (*Muntiacus muntjak*), and banteng (*Bos javanicus*) of which it might drive the coexistence among the two large carnivores.

Material and Methods

Study area

This study was carried out in UKNP, a peninsula on the south-western area of West Java within the area of 323.25 km² (6°45′ S, 105°20′ E, Fig. 1; SK.440/T.12/TU/P3/09/2017). The national park has a varied topography with terrain slopes steeper than 15° and altitude up to 620 m a.s.l. The secondary growth after the Krakatau eruption and tsunami in 1883 is the primary vegetation in UKNP. The domination of Arenga palms, which grow on thick volcanic ash, may be the result of long-past volcanic disturbance. Native plant species cover only 50 % natural vegetation on Mt. Payung and Mt. Honje area (Appendix 1). Four main types of habitat have been identified as (a) primary forest covering 50 % of the total area (dominated by *Parinari corymbosa* and *Lagerstroemia speciose*); (b) secondary forest at central lowlands (dominated by palms and other fruit trees); (c) mangrove-swamp in a broad belt along the northern side of the isthmus; and (d) beach forest (dominated by *Calophyllum inophyllum* and *Barringtonia asiatica*) restricted to the nutrient-poor sandy ridges on the north and northwest coasts of UKNP (Appendix 2).

Database construction

Camera-trap field data for Javan leopard, dholes, and their preys have been recorded from January to December 2013, including both wet and dry seasons in the area. Conditions are tropical maritime, with a mean annual rainfall of ca. 3250 mm. The heaviest rainfall occurs during the north-west monsoon (wet season) from November to April, preceding a noticeably drier period with ca. 100 mm per month during the south-east monsoon (dry season) from May to October. The
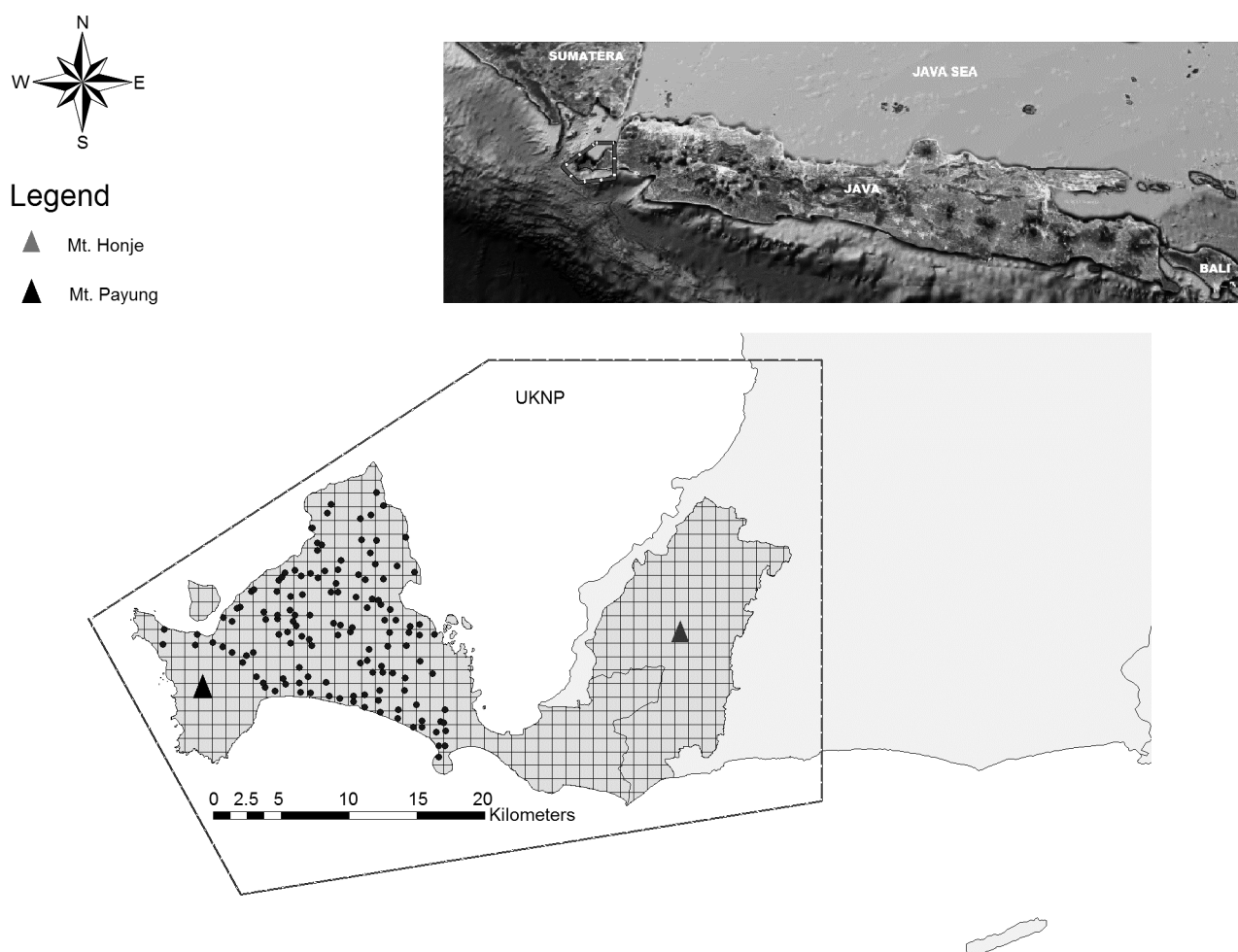
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Fig. 1. Camera trap locations in Ujung Kulon National Park (Java Island).

sampling effort was 39420 trap days and gridded into 329 1-km^2 trap stations. We used 108 camera units of Bushnell Trophy Cam 119467 and Bushnell Trophy Cam 119405. We placed the cameras at a distance of 300 to 500 m (Cruz 2002), 170 cm above the ground with a 10-20 degree angle lead to the ground (the cameras were set at 1-minute video mode with 1-minute intervals, following the standard design of camera trapping by the Rhino Monitoring Unit (RMU) team; Haryono et al. 2014). Although the camera traps were set up to monitor Javan rhinoceros and "bycatch" for Javan leopard and dhole, we believe it did not affect the captures probability. However, camera-trapping capture showed the presence of all the species that exist in UKNP, particularly for small-large sized mammals. We checked the cameras every 28 to 30 days to replace batteries, film, memory cards or malfunctioning cameras to avoid data loss. We moved the camera traps within the same grid when they did not capture any animal (zero presence) after two or three checking visits. We identified individual animals by a distinctive

mark on their body. We used spotted patterns of Javan leopards as an identifier following a double-blind observer identification protocol (Ancrenaz et al. 2012). Sequential frames of the same species were counted as one photographic event, any subsequent photograph of the same species taken within 30-minute interval was not considered as a new photographic event. We used latitude and longitude information converted into digital data in GIS using the ArcMap program to locate each photograph captured.

Data analysis
We calculated Photographic Encounter Rates (PER) for each camera trap as the ratio of the total number of independent records to the total trap nights, followed by Chi-square tests to calculate the differences between seasons.

Javan leopard density estimation
We used a Spatially Explicit Capture-Recapture framework to directly estimate Javan leopard density

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through Maximum Likelihood (SECR-ML; Efford 2004, Borchers & Efford 2008). The SECR-ML framework implemented in program DENSITY (Efford 2012) indicated the null model with negative exponential detection function as the top-ranked capture histories (Appendix 3). We selected the jackknife heterogeneity model estimator M(h) under full likelihood and homogeneous poisson distribution in DENSITY (Efford 2011). We conducted the sampling into two time periods by dividing it into each trapping campaign corresponded to 7-day sampling occasions during the wet season (January to March) and dry season (July to September). These two periods were to fulfil the assumption of the population demographic closure in SECR models. We varied the buffer size from 3 to 4 times the Root Polled Squared Variance (RPSV) to determine the space of study area. The camera surrounding should be possible to measure the scale by inter-trap movements, pooled across individuals (Efford et al. 2004). We also used a Spatially Explicit Bayesian (SECR-B, Royle et al. 2013) Capture-Recapture approach implemented in the R package SPACECAP v.1.0.6 (Singh et al. 2010) with modifications (Gopalaswamy et al. 2012). We did not calculate the density of dholes in this study since our data could lead to the high possibility of false absence. The data could give bias to the estimation density by occupancy model nor data of species-specific camera trap detected in random encounter model (Rowcliffe et al. 2008).

Species distribution modelling and validation

We used presence data of both Javan leopard and dhole to model their distribution and habitat use. We considered 15 variables in geomorphology, vegetation, climate, as well as the human impact that could act to determine both species distribution in UKNP (Appendix 4). All distance data was obtained from Indonesia's Geospatial Information Agency, Indonesian government institutions which assess and create national policies in surveys, mapping, and develop national spatial data infrastructure (Badan Informasi Geospatial Indonesia, http://www.bakosurtanal.go.id/bakosurtanal/peta-rbi). We created a distance raster using the Euclidean distance tool to measure the distance of each pixel of all landmarks and extracted it in ArcGIS 10.2.2 (ESRI, Redlands, California, U.S.A.) (Phillips 2008). Environmental layers were created using MaxEnt software (www.cs.princeton.edu/~schapire/maxent, Phillips et al. 2006) with modifications (Young et al. 2011, Rahman et al. 2017a).

We used Pearson's correlation coefficient to check multicollinearity in over-parameterisation and reduce the predictive power and interpretability, for all combinations of environmental variables (Morueta-Holme et al. 2010, Appendix 5). Variables used in the final dataset were elevation, slope, distance to river, distance to primary forest edge, distance to secondary forest edge, NDVI, annual rainfall, annual mean temperature, distance to the settlement, distance to cultivated land, and distance to the road.

We used MaxEnt v.3.3.3k with following settings: automatic feature selection, a regularisation multiplier at unity, maximum of 500 iterations, 50 replicates, and a convergence threshold of 10^{-5}. We also used a random test percentage of 10 %. We randomised in total 100 pseudo-absences of the confusion matrix for the construction in the study area. A map of the potential distribution of the species was constructed using the logistic output. The program runs with "auto features" checked (Phillips & Dudik 2008).

We measure the accuracy assessment from the Receiver Operating Characteristic curve (ROC) of each model using the Area Under the Curve (AUC) (Woodward 1999, Manel et al. 2001, Thuiller et al. 2003).

Variable contribution and response curve

We used relative contribution and permutation importance as well as jackknife test to assess the contributions of environmental variables to models (Phillips & Dudik 2008).

Interspecific interactions between Javan leopard and dholes

We used the photograph information on date and time to record the daily activity patterns and space for Javan leopard, dholes, and their prey. Capture times for each species was a random sample of photographs taken at any time of the day. We estimated the daily activity pattern overlap between Javan leopard and dholes by applying the statistical methodology developed by Ridout & Linkie (2009). We computed each species activity pattern separately using kernel density estimation or by fitting trigonometric sum distributions (Fernández-Durán 2004). All statistical analysis were using R version 2.11.1 (R Development Core Team 2009) following calculation script by Linkie & Ridout (2011). We used the $\hat{\Delta}_4$ estimator for the coefficient of overlap as recommended to calculate large sample sizes (Ridout & Linkie 2009).

Due to data overdispersion, we used two scales to describe the spatial overlap between species. The two scales were numbers of independent contacts per hour
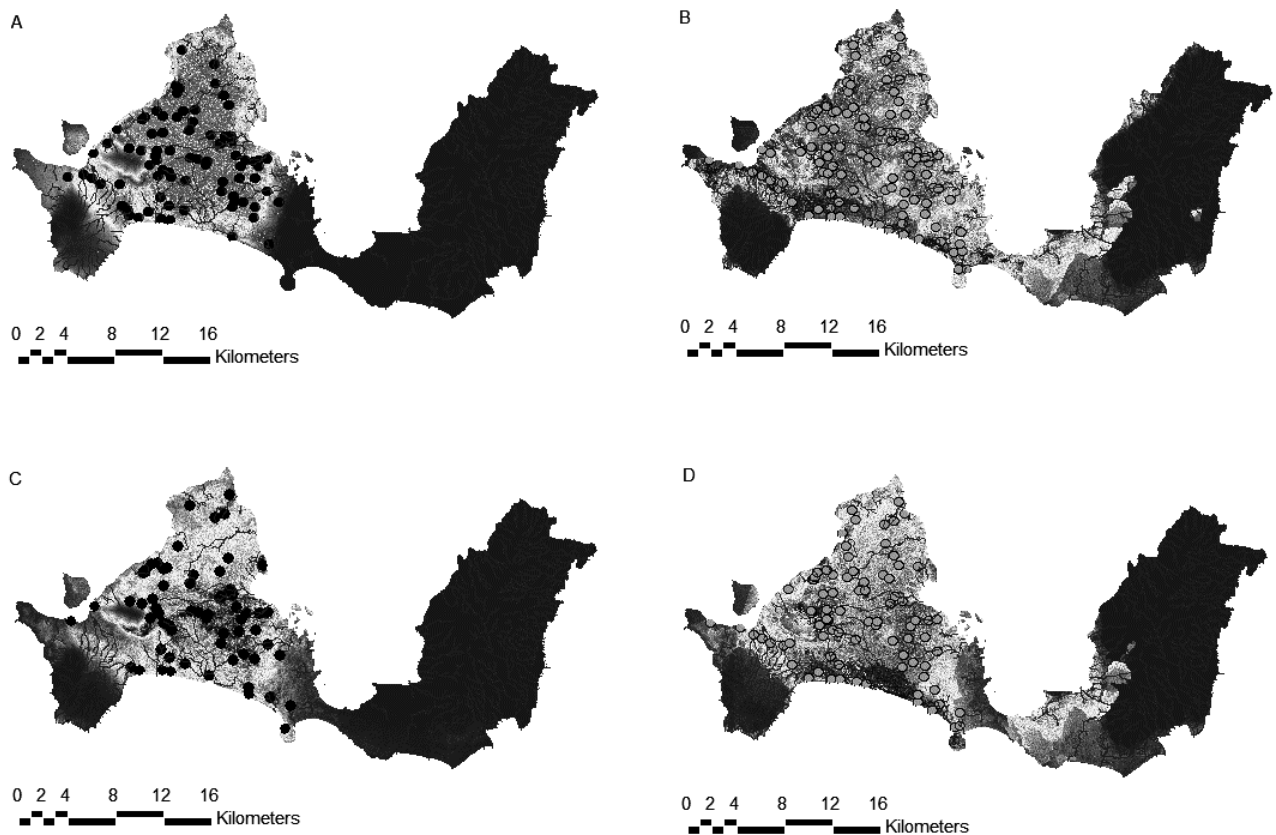
Fig. 2. Probability distribution map of Javan leopard (A, B) and dhole (C, D) in Ujung Kulon National Park in wet and dry seasons. Presence probability is displayed from low (dark grey) to high (grey). Presences recorded by the camera trapping on wet (black dots) and dry season (grey dots).
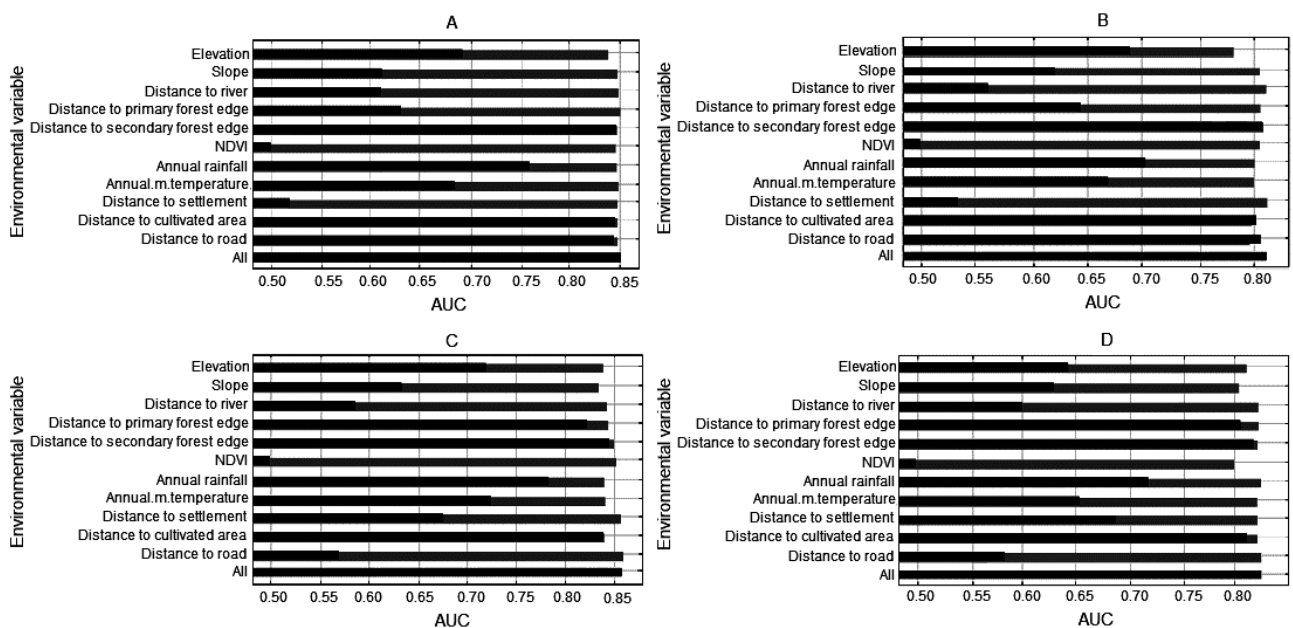
Fig. 3. Jackknife tests of AUC values of the MaxEnt models applied to Javan leopard (A, B) and dhole (C, D) in wet and dry seasons. Black bar represent model generated with this variable alone. Grey bar represent model generated without this variable. Dark grey bar represent model generated with all variables.

per habitat type (correlation type 1: the level of spatial overlap between the two species in total period) and numbers of independent contacts per location-month (correlation type 2: spatial overlap level for a shorter period on each calendar month). The differences between correlation types 1 and 2 indicated the level

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of attraction (positive value) or avoidance (negative value) in each calendar month. Furthermore, based on the results of correlation type 1 and 2, we tested daily activity rhythm in the secondary forest using binomial General Linear Models (GLM). Last, we computed Chi-square tests to compare daily and monthly activity and habitat use between species (Batschelet 1981).

Spatial overlap between Javan leopard, dholes and their prey
We used Photographic Encounter Rates (PER) from each camera trap (Carbone et al. 2001) to investigate
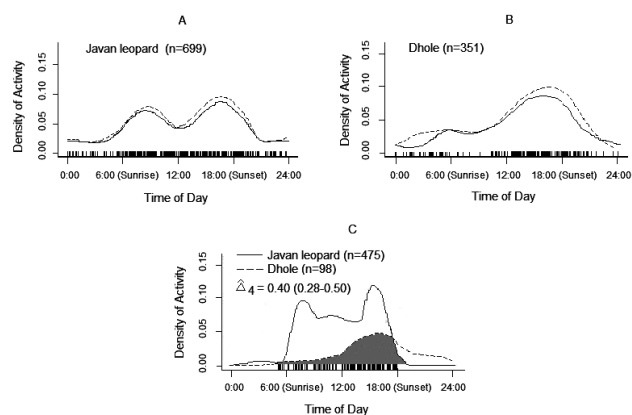

Fig. 4. Density estimates of daily activity patterns of Javan leopard (A) and dhole (B) (solid lines are Kernel-density estimates, dashed lines are trigonometric sum distributions), and daily activity patterns and overlap of Javan leopard and dhole in Ujung Kulon National Park (C).

spatial overlap between two carnivores and their prey. PER is a relative index of animal's spatial use and a crude abundance estimate (Carbone et al. 2001). We treat each camera trap as an independent spatial point. At each camera trap, the observed PER was correlated between both carnivores and prey using Spearman's rank correlation coefficient, and spatial overlap between species pairs was assessed using a Pianka index.

Results

Photographic encounter rates
We recorded 699 independent photographs of Javan leopard (229 [PER = 1.17] and 470 [PER = 2.37] in wet and dry season, respectively) as well as 351 photographs of dholes (95 [PER = 0.49] and 256 [PER = 1.29] in wet and dry season, respectively). Both species were significantly different between seasons (Javan leopard: $\chi^2 = 486.12$, df = 1, $p < 0.001$; dholes: $\chi^2 = 79.88$, df = 1, $p < 0.001$).

The density of Javan leopard
We estimated the density of Javan leopard at 11.24 and 12.80/100 km^2 for wet and dry season capture histories (SE = 3.16 and 1.99, respectively; Table 1). Bayesian analysis, whereas SECR-B implemented with SPACECAP, only the models with trap response present (behaviour model) in SPACECAP converged
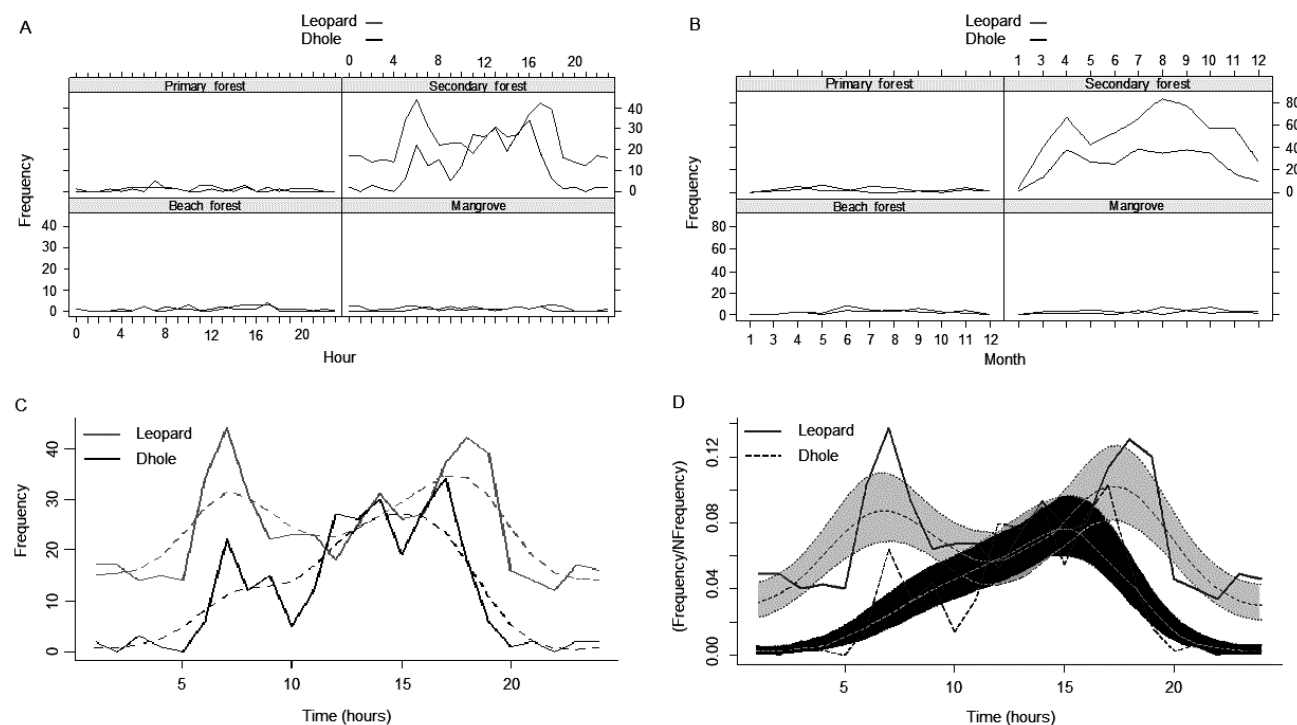

Fig. 5. Number of independent contacts per hour per habitat (A), per month per habitat (B), daily activity rhythm in secondary forest (C), as well as model predictions with 95 % confidence interval (D) applied to Javan leopard and dhole in Ujung Kulon National Park.

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for both wet and dry seasons. Our estimation with the Geweke diagnostic was < 1.6 and resulted in lower density estimates of 10.91 (SE = 2.80) and 11.54 (SE = 1.22), respectively (Table 1). Confidence intervals were large for these estimations.

Species distribution modelling and validation
Distribution models for both species and seasons were performed well. All AUC values were more significant than 0.797 (Table 2, Appendix 6). Models identified a high probability of the presence area within study sites. In almost the whole TNUK area, except the high mountains at the southwest on both seasons, we have located high-predicted suitable conditions for Javan leopard (Fig. 2A, B) and dholes (Fig. 2C, D).

Significant explanatory variables
In wet and dry seasons, Javan leopard showed the most significant relative contribution at a distance to secondary forest edge (85.7 % and 88.6 %, respectively, Table 3) followed by distance to the nearest road (5 % and 6.5 %, respectively). Furthermore, as on permutation importance, distance to the settlement showed the most significant value in both seasons (50.4 % and 53.1 %, respectively) followed by distance to the cultivated area (26.7 % and 22.9 %, respectively). Distances to settlement and cultivated area have negatively influenced the occurrence of Javan leopard in contrast to distances to the secondary forest edge and road. The response curves were roughly unimodal for distance to secondary forest edge and bimodal for distance to the road in both seasons (Appendix 6A, B). As of jackknife tests suitability model were showing the highest gain when "distance to secondary forest edge" was used alone, while "distance to settlement" most increased the gain when it was omitted (Fig. 3A, B).

On the other hand, dholes showed the most relative contribution at a distance to secondary forest edge in wet and dry seasons (84.9 % and 87.9 %, respectively), followed by distance to road (6.5 % and 7 %). The most significant variable on permutation importance distance to the primary forest was the edge (46.2 % and 59 %, respectively) followed by the cultivated area (29.2 % and 25 %, respectively). The distance to the primary forest edge positively influenced the occurrence of dholes contrary to cultivated area. Our response curves results in both seasons showed roughly unimodal for distance to secondary forest edge and bimodal for distance to the road (Appendix 6C, D). Jackknife tests suitability models showed the "distance to forest edge

secondary" as the highest gain when it was used alone. The "distance to the road" will increase the gain when it was omitted (Fig. 3C, D).

Interspecific interactions between Javan leopard and dhole
Kernel density and trigonometric sum estimate activity patterns for the two species. It has shown similar patterns within Javan leopard and dholes (Fig. 4A, B; respectively). We identified the low degree of daily activity overlap between Javan leopard and dhole (estimated overlap coefficients < 0.35, $\hat{\Delta}_4 = 0.40$; Fig. 4C). Both species had non-overlapping spatial activity in four habitat types using a different peak of hourly distribution pattern.

Primary and beach forest, as well as mangrove area, are regularly used throughout the year. Whereas in the secondary forest, high activity was recorded from March to September and December to January for its lowest (Fig. 5A, B). The captured frequency of Javan leopard and dholes were positively correlated at secondary forest indicating that both species used the same areas (Fig. 5C). Although it did not show both species appear at the same time in the same areas. Javan leopard showed a bimodal pattern with equal higher activities at dawn and dusk.

On the contrary, dholes showed the same pattern with high activity in the afternoon and late afternoon (3 to 4 p.m.). The model ignored the small activity peak at dawn due to a 95 % confidence interval (Fig. 5D). Differences between spatial activities were significant for both species (daily activity: $\chi^2 = 131.33$, df = 23, $p < 0.001$; monthly activity: $\chi^2 = 13.46$, df = 10, $p < 0.05$; habitat use: $\chi^2 = 1.58$, df = 3, $p < 0.05$).

Spatial overlap between Javan leopard, dholes and their prey
Javan leopard exhibited positive spatial correlation with dholes (Table 4). Java mousedeer spatially correlated with Javan leopard but did not correlate with dholes. Dhole spatially associated with boar, red muntjac, and banteng. In overlap encounter, banteng is more spatially overlapping with dholes than Javan leopard. Nevertheless, we did not have overlap encounter between Javan leopard and dholes feeding behaviour.

Discussion
This study reports an extensive dataset on the main carnivores in Java Island, including population size estimation and spatial overlap between Javan leopard and dhole, as well as their putative prey species.

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Table 1. The Javan leopard density estimated from spatially-explicit capture-recapture methods. Estimation was obtained from maximum likelihood (SECR-ML) methods in program DENSITY and Bayesian (SECR-B) methods in SPACECAP.

Program	Capture histories	Density (Javan leopards/100 km²)	SE (Javan leopards)
DENSITY	Wet	11.24	3.16
	Dry	12.80	1.99
SPACECAP	Wet	10.91	2.80
	Dry	11.54	1.22

Table 2. The AUC and standard deviation for each species model in two seasons at Ujung Kulon National Park.

Species	Season	Number of photographs	AUC	Standard deviation
Javan leopard *Panthera pardus melas*	Wet	240	0.836	0.079
	Dry	495	0.825	0.073
Dhole *Cuon alpinus*	Wet	161	0.848	0.100
	Dry	434	0.797	0.080

Table 3. The relative contribution (RC) and permutation importance (PI) of each environmental variable. These were for each species as in average over 50 replicates. Values are normalised to give percentages. Bold numbers are showing the two highest percentages.

Environmental variable	Javan leopard				Dhole			
	Wet season		Dry season		Wet season		Dry season	
	RC	PI	RC	PI	RC	PI	RC	PI
NDVI	1.5	0.6	0	0.2	1	0.7	0	0.1
Elevation	0.3	4.3	1.4	7	1.3	9.9	1	7.1
Slope	0.2	2.2	0.3	5.5	0.3	1.9	0	0.8
Distance to nearest river	0	0.4	0.1	0.8	0	0	0	0
Distance to primary forest edge	0.2	1.3	0	0.1	0.1	**46.2**	0.1	**59**
Distance to secondary forest edge	**85.7**	0	**88.6**	0	**84.9**	0	**87.9**	0
Distance to nearest settlement	1.5	**50.4**	1.3	**53.1**	0.8	0.8	1.2	1.9
Distance to nearest cultivated area	4.5	**26.7**	1.1	**22.9**	4.3	**29.2**	1.4	**25**
Distance to nearest road	**5**	7.6	**6.5**	3.1	**6.5**	8.9	**7**	0.8
Annual mean temperature	1.1	6.3	0.1	3.5	0.4	0.1	0.9	2.1
Annual rainfall	0	0.1	0.5	3.7	0.3	2.3	0.4	3.2

Table 4. Spatial use of both sympatric carnivores and their primary prey in Ujung Kulon National Park ([a]$P < 0.01$, [b]$P < 0.05$).

Variables	Spatial use	
	Spearman correlation	Pianka index
Javan leopard and dhole	0.28[b]	49
Javan leopard and Java mousedeer	0.13[b]	55
Javan leopard and wild pig	−0.15	53
Javan leopard and red muntjac	0.30[a]	39
Javan leopard and banteng	0.24	55
Dhole and Java mousedeer	−0.03	39
Dhole and wild pig	0.18[b]	51
Dhole and red muntjac	0.15[b]	63
Dhole and banteng	0.36[a]	70

Although our data covers only a single national park on the western tip of Java Island, the robust sampling design and the variety of surveyed habitats support a more considerable extent to our results which may constitute a basic knowledge for other areas in Java and the whole species' range. We are surprised by a large number of Javan leopard and dhole photographs that were conducted on this study, considering these species are rare to be found. To date, there is no report on population data of dholes anywhere in their natural habitat. A study in Baluran National Park also estimated a yearly decline population of Javan leopard (Pudyatmoko 2005).

Our result showed a lower number of records in the wet season for both species compare to the dry season. It is possibly related to a lower level of activity caused by higher food availability. Therefore, the food availability during the dry season is scarce. This relative scarcity is leading to a broader movement of prey species and increasing the encounter probability with its predator (Pontes & Chivers 2007, Rahman et al. 2017b). Two leopard species were reported to live in sympatry, whereas interspecific resource competition could develop at the junction of closed and open habitats, through the use of the same prey species, especially if their availability is limited (Lovari et al. 2013). Examples in tropical region whereas carnivores, e.g. ocelots (*Leopardus pardalis*) used larger ranges during the dry season to follow the movement of their prey (Ludlow & Sunquis 1987).

In contrast, in Khao Yai National Park (KYNP) Thailand, leopard cats used larger areas during the wet season than dry season (Austin et al. 2007). An essential seasonal difference in KYNP was the lack of seasonal flows during the dry season which led to a lack of water sources and affect the behaviour patterns of leopard cats and their prey. These seasonal changes of range patterns are influenced by changes in small mammal distributions (Rabinowitz 1990). The time dedicated to predators for searching and obtaining prey is inversely proportional to its abundance (Carbone & Gittleman 2002).

The expected Javan leopard density in UKNP, which lies between 10.91-12.80/100 km^2, is higher than the estimated densities of Javan leopard in other areas in Indonesian rainforests, (i.e. one individual/5.9-13.6 km^2 in Gunung Gede Pangrango National Park; [Ario et al. 2009] and one individual/6.5-6.7 km^2 in Gunung Halimun-Salak National Park; [Harahap & Sakaguchi 2005, Ario 2007, respectively]). It is comparable, although these previous studies are using data from a full count of camera traps using classical MMDM based CR model (without considering the space and movement of the species) (Ario 2006, 2007, Ario et al. 2008, 2009). Furthermore, the actual population might be higher since no survey had been reported yet in other areas such as Mt. Honje (167.25 km^2). The presence of the Javan leopard was reported in the year 2013 in this area (UKNP 2013). Our study provided population density estimates of Javan leopard ca. 35.23-41.37 individuals. The high densities of Javan leopard in UKNP appear because of the lower edge effect present in this area, and it was also close to human access. Besides, the high availability of prey animals supports the population growth of this species in UKNP.

Identifying areas in wet and dry seasons with high probability presences of both sympatric carnivores species will be a valuable information tool to determinate conservation priority areas. It includes subsequently direct ranger patrols, anti-poaching efforts, and anti-encroachment operations. The suitability distribution maps generated by our models show both predicted areas of the high and low presence probability for each species. Moreover, it also provides an understanding of relevant natural and anthropogenic variables which support the occurrence of the two carnivores. Our maps identified a high level of similar areas within UKNP combined with the high predicted probability of both species' presence.

Our study explicitly stated that both carnivore species have strong preferences for forests located in lowland areas. They are providing a high primary source of plant diets for their prey (Harmsen et al. 2011). Our habitat models show that Javan leopard and dholes are mainly concentrated far from cultivated areas and settlements, farther from human disturbances. The abundance of potential domestic prey associated with human-settlements might attract predators, and this interaction could result in conflict with humans (Athreya et al. 2016). Regrowth of dominant fruit tree canopies is abundant in secondary forest areas, which are conducive to herbivores' prey species (Brown & Lugo 1990, García-Marmolejo et al. 2015), i.e. muntjac (one of the prey species in UKNP) (Lovari & Mori 2017, Rahman et al. 2017a). Muntjacs feed on fruits, buds, tender leaves, flowers, herbs and young grass as their daily food preference (Oka 1998). While, our result is dissimilar with previous studies reporting that leopard and dholes are adaptable, using wide varieties of habitats as well as feeding on a range of wild and domestic prey (Athreya et al. 2013, Kamler et al. 2015). The abundance of wild preys and low

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human pressure in UKNP offers both Javan leopard and dholes an optimal forest niche. However, a recent study in the area showed that red muntjac tends to come closer to the cultivated areas (e.g. cassava, tubers, corn, and others) which is more attractive in the dry season (Rahman et al. 2017a).

Furthermore, our results showed insignificant through each variable (e.g. NDVI, elevation, slope, and distances to the river, annual mean temperature and annual rainfall). It is likely because the variables were too small within the studied area or fall within the usual range for both carnivore species. UKNP is an example of lowland tropical rainforest with low variations in elevation and slope (with maximum height of 800 m; S. Hedges, pers. comm.). Elevation was correlated negatively significant to the number of dholes' presences (Namgyal & Thinley 2017). The positive effects of NDVI may not be closely related to the carnivore species, but rather to the presence of prey animals that are strongly dependent on the forests. From ca. 70 % of all forest habitat types in UKNP, secondary forest were highly dominant and strongly associated with the presence of prey animals.

Javan leopard and dhole have highly overlapping ranges, with several same locations visited. Although the range size was not possible to be estimated from the camera-trap dataset, we observed the fluctuating presence and absence of both species across our camera network. Record periods of up to 12 months indicated both species were able to shift ranges across large areas. This shifting occurred when prey occupied a larger area due to reduced grazing area in dry season. Still, Javan leopard and dhole were captured within the same area. Our result shows Javan leopard occupying the same area with dhole simultaneously and no evidence of spatial avoidance. Avoidance happens only from dholes to the Javan leopard presence in the area and not *vice versa*. The spatial distribution of several mesopredators is a hierarchical process at the individual level. The hierarchy starts from the driven level to the acquire resources which then enhanced avoidance by predators (Broekhuis et al. 2013).

Conversely to the spatial overlap, we found evidence of temporal avoidance between Javan leopard and dholes. The avoidance is more passive than active because it relies on differences in activity patterns, although there is a small common active period. As in our study, the Javan leopard is reported to be a crepuscular hunter (Harahap & Sakaguchi 2005). Although the examination data cannot reveal whether avoidance was mutual, it is likely that the physically smaller dhole avoid Javan leopard, facilitating some temporal separation from the Javan leopard. Our results show that Javan leopard and dholes avoid one another less than they avoid conspecifics, we have never found both of species in the same frame at one time.

Javan leopard has significant definite spatial overlap with Java mousedeer and red muntjac, while dholes have overlapped activities with wild boar and banteng. The diet of the Javan leopard, compared to dhole, have a longer duration of feeding activity with broader feeding choices due the leopard is morphologically adapted to kill large prey including small preys (Hayward et al. 2006). Also, we observed predation activity by Javan leopard on Javan langur (*Trachypithecus auratus*). We obtained four photos from our camera trap sequence whereas leopard had ambushed the Javan langur. Leopard has been reported to also consume a high percentage of monkey (Ario 2006, Athreya et al. 2016, Lovari & Mori 2017).

On the other hand, dholes were almost exclusively diurnal hunters (Nurvianto et al. 2015). Our camera trap at UKNP showed a group of dholes preying on a banteng calf by separating it from its mother. Compared to other prey species such as muntjac and sambar (*Rusa unicolor*), dholes activity pattern was significantly different, an exception to wild boar (Kamler et al. 2012). Dholes consumed a bigger size of preys to meet their needs of diet as pack hunters. Dholes' exhibit similar predator to prey ratios, in contrast to solitary hunters' Javan leopard (feed on equal or slightly smaller size) (Hayward et al. 2014).

Conservation impact

Our study emphasised the feasibility of documenting species-habitat relationships of two sympatric carnivores in the critical conservation landscape of UKNP, Indonesia. We demonstrate long-term/ intensive field sampling surveys to estimate the density of Javan leopard. It adequately addresses the impact of associated threats including other environmental variables on Javan leopard and dholes' spatial distribution as well as habitat type, competitor, medium-large sized prey, and climatic data. We provide the first reliable and precise estimates of Javan leopard density through a combination of camera trapping and capture-recapture modelling. This study represents a way forward in population monitoring for effective conservation of threatened and endangered top predators. We propose the "hotspots" area of

Javan leopard density as one of the highest population in UKNP. We highlight the need to develop further rigorous approaches to improve the measurement of species density across their distributional range. Our study has applications for habitat prioritisation and recovery of native habitat.

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Supplementary online material

Appendix 1. Four main habitat types in Ujung Kulon National Park.

Appendix 2. Distribution of the Krakatau ash in Ujung Kulon National Park.

Appendix 3. Program DENSITY model selection and estimates (using Mh jacknife estimator) for Javan leopard left capture histories for camera trap study in Ujung Kulon National Park, Indonesia. Models were ranked based on Akaike Information Criterion adjusted for small sample sizes (AIC$_c$) and AIC$_c$ weights. K = number of parameters, g0 = capture probability at home range center, sigma = spatial scale over which detection declines.

Appendix 4. The environmental variables was considered to influence Javan leopard and dholes distribution in Ujung Kulon National Park.

Appendix 5. Pearson's correlations between the environmental variables used in the distribution modelling for Javan leopard and dholes in Ujung Kulon National Park.

Appendix 6. Response curves and AUC values of the MaxEnt models applied to Javan leopard (A, B) and dholes (C, D) in the wet and dry seasons (http://www.ivb.cz/folia_zoologica/supplemetarymaterials/rahman_et_al_appendixes1-6.doc).