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Factors affecting seasonal habitat use, and predicted range of two tropical deer in Indonesian rainforest

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ABSTRACT

There is an urgent recognized need for conservation of tropical forest deer. In order to identify some environmental factors affecting conservation, we analyzed the seasonal habitat use of two Indonesian deer species, *Axis kuhlii* in Bawean Island and *Muntiacus muntjak* in south-western Java Island, in response to several physical, climatic, biological, and anthropogenic variables. Camera trapping was performed in different habitat types during both wet and dry season to record these elusive species. The highest number of photographs was recorded in secondary forest and during the dry season for both Bawean deer and red muntjac. In models, anthropogenic and climatic variables were the main predictors of habitat use. Distances to cultivated area and to settlement were the most important for *A. kuhlii* in the dry season. Distances to cultivated area and annual rainfall were significant for *M. muntjak* in both seasons. Then we modelled their predictive range using Maximum entropy modelling (Maxent). We concluded that forest landscape is the fundamental scale for deer management, and that secondary forests are potentially important landscape elements for deer conservation. Important areas for conservation were identified accounting of habitat transformation in both study areas.

1. Introduction

There can be little doubt that the lowland tropical forests, even though occupy only 7% of the land area, are the most species-rich of all terrestrial ecosystems and suffer the highest deforestation rates worldwide (Corlett and Primack, 2010; FAO, 2010; 2011; World Resources Institute, 2011; Hofsvang, 2014). Tropical forest degradation and fragmentation dramatically transform natural dynamics, potentially triggering species extinctions, decreasing survival, modifying habitat use and species distributions (Fahrig, 2003). Fragmentation impacts habitat availability and wildlife species, depending on their particular habitat requirements and their ability to move through the landscape (Ojasti, 2000; Turner et al., 2001). For example, habitat fragmentation caused by anthropogenic activities is the main factor that induces habitat use changing by ungulates (Tejeda-Cruz et al., 2009; García-Marmolejo et al., 2015), or constrain long-distance movement of Mongolian gazelles (*Procapra gutturosa*) and Asiatic wild asses (*Equus hemionus*) (Ito et al., 2013). Knowledge about the habitat and the range of species is crucial for designing sound management strategies of biodiversity conservation (Arzamendia et al., 2006; Kumar et al., 2010).

Information on which a range is occupied or avoided by organisms improves our understanding of how they meet their requirements for survival and reproduction (Manly et al., 2002). Habitat use by mammalian herbivores such as deer species is considered as an optimization process that involves factors such as body size, population density, competitors, predators, food availability, landscape, and microclimate (Morrison et al., 1992; Ofstad et al., 2016). For example the use of open habitats landscape by red brocket and white-tailed deer may be associated with its large body size and the structure of male antlers, which influence movement and feeding (Bolaños and Naranjo, 2001). While, the mule deer changed their habitat use after coyotes were introduced into the enclosure (O'Brien et al., 2010), and sika deer increased their relative use of habitat in lower quality during the high-density

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period (Borkowski, 2011). Furthermore, habitat use in dry season being most sensitive to competitive interactions within and between grazers species in an African savanna (Macandza et al., 2012). In red deer, neither habitat use nor home-range behaviour, especially those of males, was closely related to the pattern of spatial and seasonal variation in food resources (Lazo et al., 1994).

For predicting species habitat use and range several statistical models exist: general linear modelling/GLM (McCullagh and Nelder, 1989), algorithmic modelling (Ripley, 1996), beyond classical regression (Manly et al., 1993), genetic algorithm for rule set production/GARP (Stockwell and Peters, 1999), ecological niche factor analysis/ENFA (Hirzel et al., 2002), Bioclim (Beaumont et al., 2005), maximum entropy modelling/Maxent (Phillips et al., 2006), and multiple factor analysis/MFA (Calenge et al., 2008). Maxent, one of the most commonly used presence-only modelling for inferring species distribution, habitat use and environmental tolerances from occurrence data, allows users to fit models of arbitrary complexity (Warren and Seifert, 2011). Moreover, Maxent has been described as especially efficient to handle complex interactions between response and predictor variables (Elith et al., 2006, 2011). It is commonly used in studies in tropical regions (Cayuela et al., 2009), and is little sensitive to small sample sizes (Wisz et al., 2008).

Mammal fauna such as deer species have been proposed as good indicators of the integrity of natural communities because they integrate a number of resource attributes, and thus may show population declines quickly if one is missing (Escamilla et al., 2000). In addition, Smith et al. (1993) estimated that almost 79% of the tropical deer species are at risk of extinction and become the most endangered mammal group.

The “Critically Endangered” Bawean deer *Axis kuhlii* (Temminck, 1836) is one of the Indonesian ungulate species threatened by human activities (Semiadi et al., 2013). This deer lives only on the 200 km^2 Bawean Island (Lachenmeier and Melisch, 1996; Grubb, 2005) and is the most isolated deer in the World (Blouch and Atmosoedirdjo, 1987; Semiadi et al., 2013). It is listed in Appendix I of CITES (2009). On the contrary the “least concern” red muntjac *Muntiacus muntjak* (Zimmermann, 1780) is a locally common species (Davies et al., 2001) with varying levels of threat. Red muntjac is among the most widespread tropical cervids (Chasen, 1940; Groves, 2003; Meijaard, 2003), ranging from Pakistan to Indonesia, through all south-eastern Asia (Mattioli, 2011). In Indonesia populations of red muntjac persist in many areas where there is some forest cover (Whitten et al., 1996), on Bali, Java, southern Sumatra and Kalimantan Islands. Both species looks very similar in terms of body size and sexual dimorphism, and they are considered to be typical and flagship solitary species of tropical forests (Blouch and Atmosoedirdjo, 1978; Oka, 1998; Mattioli, 2011).

Like many other tropical forest cervids, Bawean deer and red muntjac are difficult to monitor because of their elusive behaviour. Recently, camera-traps have become an important tool for monitoring terrestrial rare and cryptic species which are difficult to observe in tropical rainforests (Karanth, 1995; Karanth and Nichols, 2002; Tobler et al., 2008). Camera trapping was also successful in determining abundance, habitat use and range of elusive ungulates (Bowkett et al., 2007; Rovero and Marshall, 2009; Krishna et al., 2009; Tobler et al., 2009). They proved to be useful for recording deer with high detection efficiency (Rovero et al., 2014).

In tropical rainforest, the lowland forest ecosystems are considered optimal habitats for deer species. Within these ecosystems primary forests are reported to be highly productive for a wide variety of vertebrates, particularly for mammalian species. Furthermore ‘specialist’ species associated with these forests are more vulnerable to disturbance and eradication (Rijksen, 1978; Yasuda et al., 2003; Meijaard et al., 2005) usually bestowing a higher conservation status upon them. We tested the hypotheses that (i) both deer species are highly dependent of primary forests versus other forest types, (ii) undisturbed protected forest areas are essential for their conservation. We used Maxent to model the habitat use and predict the range of Bawean deer for testing these hypotheses in Bawean Island Nature Reserve and Wildlife Sanctuary and red muntjac in Ujung Kulon National Park (Indonesia).

2. Material and methods

2.1. Study areas

We studied Bawean deer in Bawean Island, an isolated island in Java Sea (5°40′-5° 50′S; 112° 3′-112° 36′E, Fig. 1). According to the classification of Schmidt and Ferguson (1951), Bawean Island climate is categorized in type C (Semiadi, 2004). Within the island mean temperature varies between 22 °C and 32 °C, and relative humidity ranges between 50% and 100% (Semiadi, 2004). The mean annual rainfall reaches 2.298–2.531 mm on the southern coast; rainfall is more abundant during the north-west monsoon from the end of October until April (wet season) than during the south-east monsoon from May to October (dry season). The protected area of Bawean Island Nature Reserve and Wildlife Sanctuary (BINR-WS) of ca. 725 ha (nature reserve) and ca. 3.832 ha (wildlife sanctuary) is characterized by a steep topography (with terrain slopes > 60°) and a wide altitudinal gradient (1–630 m). The BINR-WS constitutes one of the last strongholds in the country for endemic medium-large mammalian ungulates such as the Bawean deer and Bawean warty pig *Sus verrucosus blouchi* (Boie, 1832).

The main vegetation type is a tropical evergreen rainforest which can be divided into four major forest types: primary forest, secondary forest, teak (*Tectona grandis*) forest, and shrub (Table 1, Appendix 1A). The BINR-WS protects one of the small patches of evergreen rainforest in Indonesia (ca 23% of the Bawean Island**),** including teak plantations (60% of this area). This habitat type is globally endangered by deforestation and climate change (Semiadi, 2004; Rahman et al., 2017). The remaining natural forests are confined to the steep sides and top of the higher hills and mountains, often occurring as islands surrounded by teak.

We studied Red muntjac in Ujung Kulon National Park (UKNP), a peninsula of ca. 76.214 ha at the extreme southwestern tip of Java Island, Indonesia (6°45′S; 105°20′E). UKNP climate is categorized in type A (Hommel, 1987). The mean temperatures range between 25 °C and 30 °C and relative humidity ranges between 65% and 100% (Blower and Van Der Zon, 1977; Hommel, 1987). Conditions are tropical maritime, with a mean annual rainfall of ca. 3.250 mm. The heaviest rainfall occurs during the north-west monsoon (wet season) from October to April, preceding a noticeably drier period with ca. 100 mm per month during the south-east monsoon (dry season) from May to September. The Ujung Kulon National Park has varied topography (with terrain slopes > 15°) and a wide altitudinal gradient (0–620 m). The UKNP constitutes one of the last strongholds in the country for endemic large mammalian ungulates such as the Javan rhino *Rhinoceros sondaicus* (Desmarest, 1822).

The main vegetation is a tropical evergreen rainforest, which has suffered a number of anthropogenic and natural modifications. It is mainly secondary growth, following the destructive Krakatau eruption and tsunami of 1883. The main habitat types are primary forest, secondary forest, mangrove-swamp and beach forest (Table 1, Appendix 1B). The Arenga palms, which grow on thick ash, may be dominant as a result of long-past volcanic disturbance. As a result, the natural vegetation cover, now occupies only 50% of the total area, and is largely confined to the Mt. Payung and Mt. Honje massifs.

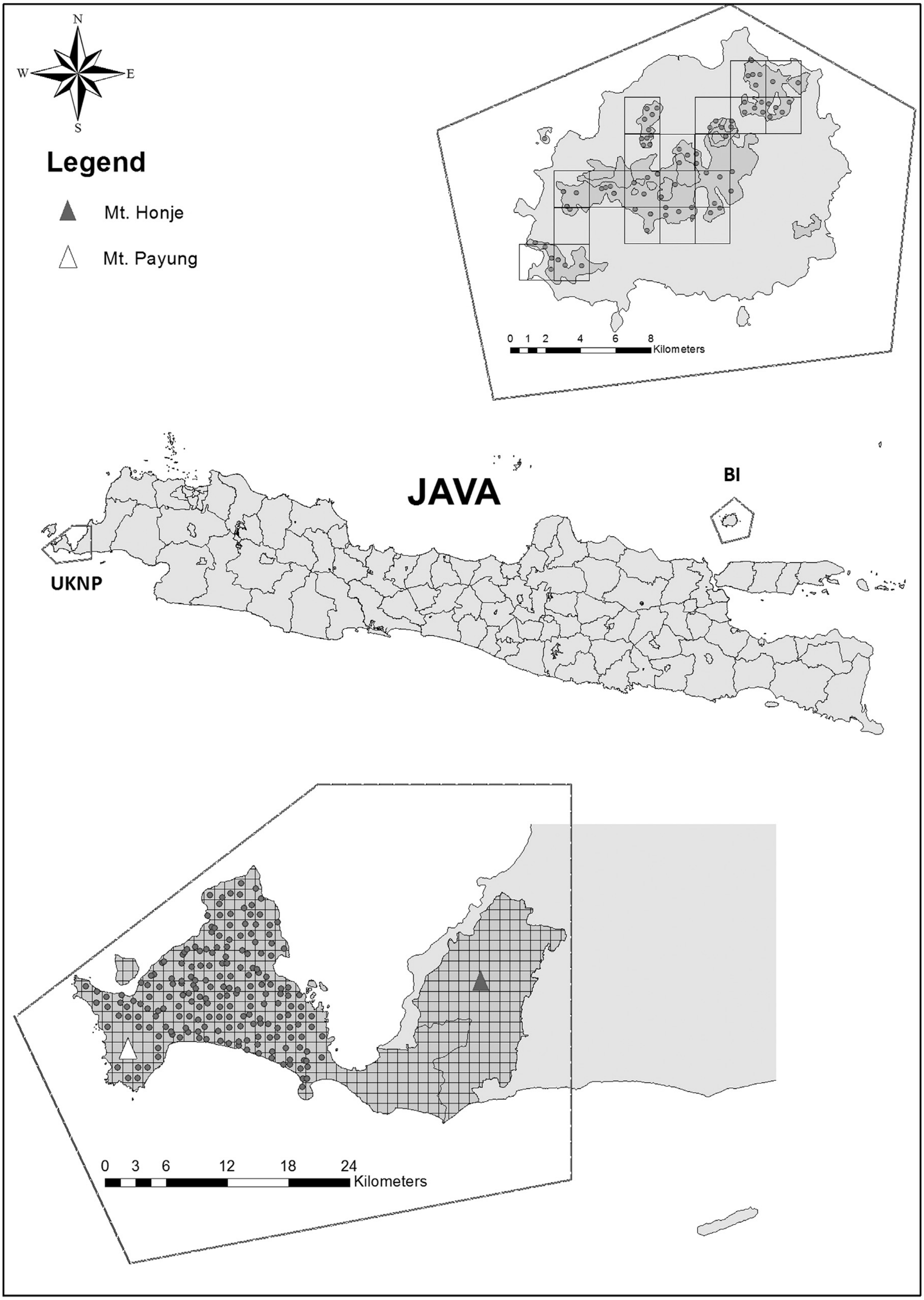

Fig. 1. Camera trap locations within the two Indonesian study sites: Bawean Island (BI, black dots, upper map) and Ujung Kulon National Park in Java Island (UKNP, black dots, lower map).

Table 1
Habitat types monitored for Bawean deer and red muntjac activity with camera trapping surveys, respectively from March to November 2014 in Bawean Island Nature Reserve and Wildlife Sanctuary and from January 2013 to July 2014 in Ujung Kulon National Park, Indonesia. Both of study site have a similary of categorical of habitat type, but with different composition.

Study site	Habitat	Description
Bawean Island Nature Reserve and Wildlife Sanctuary	Primary forest	Old forest subject weakly disturbed by human activities and generally not easily accessible; both tree and understory species vary greatly from one mountain to another. Most two common trees include *Anthocephalus indicus*, *Ficus variegate* and the understory is an assemblage of tree saplings and low species such as *Leea indica, Antidesma montanum*.
	Secondary forest	Most of forests are patchy within teak plantations, mainly where plainting failed. It is characterized by an overstory dominated by fast-growing fruit trees canopy, most two tree composed included *Ficus variegata*, and *Macaranga tanarius* and understory is quite dense, made up species such as *Leea indica*, *Ficus* spp.
	Teak forest	Host the same species as secondary forests, but large trees are mainly teak and understory is generally less dense because of occasional fire.
	Shrub	Poor, sandy soil and are characterized by small woody plants, mainly *Melastoma polyanthum* and *Eurya nitida*.
Ujung Kulon National Park	Primary forest	Occupies 50% of the total area, open canopy with numerous emergents up to 40 m high. Dominant tree species are *Parinari corymbosa* and *Lagerstroemia speciosa* and understory includes palms such as *Arenga obtusifolia* and *Calamus* spp.
	Secondary forest	Concentrated in central lowlands, dominated by palms and other fruit trees, such as *Arenga pinata*, *Arenga obtusifolia*.
	Mangrove-swamp	Occurs in a broad belt along the northern side of the isthmus, extending northwards as far as the Cikalong river, as well as north of Pulau Handeleum and northeast coast of Pulau Panaitan. Tree species include *Sonneratia alba* and *Lumnitzera racemosa*.
	Beach forest	Occurs on nutrient poor sandy ridges on the north and northwest coasts of Ujung Kulon, and is typified by such species as *Calophyllum inophyllum* and *Barringtonia asiatica*.

2.2. Survey methodology

Given the lack of information about the extent of home range of both deer species from previous studies and according to the areas and habitat types to be surveyed, and the number of available camera-traps, BINR-WS was gridded into 20 2-km^2 trap stations (10 in primary forest, 5 in secondary forest, 3 in teak forest and 2 in shrub) and UKNP was gridded into 329 1-km^2 trap stations (112 in primary forest, 84 in secondary forest, 54 in mangrove-swamp and 78 in beach forest). Camera-traps with heat-in-motion detectors were used to continuously record over the 24-h activity of the target species and set to record date and time of all photos. In BINR-WS we mounted 20 units of Bushnell Trophy Cam HD Max analog cameras on trees, positioned 30–50 cm above the ground to record both small and large animals. In UKNP, we used 108 units Bushnell Tropy Cam 119467 and Bushnell Tropy Cam 119405 analog cameras 170 cm above the ground with a 10–20° angle lead to the ground (following the standard design of camera trapping by Rhino Monitoring Unit [RMU] team) that were positioned to survey the Javan rhino. These differences in camera trapping did not affect the photographic capture probability of both deer species.

Positioning camera-traps in each trap station or grid adopted the methodology of Karanth and Nichols (1998) in both study areas. Cameras were set up in a way to cover the whole study area by applying a buffer equivalent to half of the mean maximum distance moved (1/2MMDM). This means that any individual in the study area had a probability greater than zero to be photographed by at least one camera. Because our goal was to obtain as many photographs as possible in each grid, when a camera did not capture any object (zero presence), we changed its location in the same grid.

Field surveys were carried out during 9 months (March to November 2014) and 19 months (January 2013 to July 2014) in BINR-WS and UKNP, respectively. The sampling periods included both wet and dry seasons. Cameras were checked once every 21–30 days, including replacing battery and memory card, and even the camera-trap in case of malfunction in order to avoid loss of data. Each photographed animal was identified to species. Photographs whose quality did not allow an accurate identification were excluded from the dataset. Sequential frames of the same species were counted as one photographic event, and unless individual identification was possible, any subsequent photograph of the same species taken within 1 h was not considered a new photographic event. Individual identification possibly relied on permanent scars (Jacobson et al., 1997), neck thickness in proportion to body (González-Marín et al., 2008), the presence and form of antlers or the presence of fawn in the case of females. The location of each photograph was recorded by latitude and longitude and converted into digital data in GIS using ArcMap program. Sampling effort during the survey was 5.500 trap days in BINR-WS and 62.316 trap days in UKNP.

2.3. Data analysis

2.3.1. Photographic encounter rates

We calculated photographic encounter rates (PER) per grid as: PER = total number of photos * 100/sampling effort (camera-trap days). As the number of photographs significantly differed between seasons (Chi-square tests), we compared the seasonal PER among habitat types in each study site using Kruskal-Wallis tests adjusted for equal numbers and *post hoc* tests for multiple comparisons ($\alpha = 0.05$).

2.3.2. Species distribution modelling and validation

For modelling the distribution and habitat use of both deer species, we used presence records of deer as dependent variables. Then, we selected 15 environmental variables, which we considered to influence deer distribution based on previous studies. These variables were classified into four classes: 1) physical variables such as elevation, slope and distance to the nearest river (Debeljak et al., 2001; Patthey, 2003), 2) resources such as land cover (distance to primary forest and secondary forest) and vegetation productivity (Schutz et al., 2003), 3) anthropogenic disturbance such as distance to settlement, cultivated area and road (Patthey, 2003), and 4) climatic variables such as annual rainfall, rainfall of the wettest month, rainfall of the driest month, annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month (Solberg et al., 2001; Hovens and Tungalaktuja, 2005).

Elevation data were downloaded as an ASTER global digital elevation model (DEM). A 90 × 90 m digital elevation model was downloaded from Landsat 8 (http://earthexplorer.usgs.gov or http://srtm.csi.cgiar.org) from which slopes were generated using the slope function in ArcGIS (Jarvis et al., 2008). Data for rivers, land cover, roads were obtained from the Badan Kordinasi Survei dan Pemetaan Nasional (http://www.bakosurtanal.go.id/bakosurtanal/peta-rbi). Vegetation productivity was measured as the normalized difference vegetation index (NDVI, cf. Hansen et al., 2009). Climatic variables were downloaded from the WorldClim database (http://worldclim.org/bioclim). These data are derived from monthly temperature and rainfall values recorded between 1950 and 2000 from a global network of climate stations. All layers were projected into WGS 1984 Zone 49 South (Bawean Island) and WGS 1984 Zone 48 South (Ujung Kulon National Park).

We extracted distance values in ArcGIS 10.2.2 (ESRI, Redlands, California, USA) to create environmental layers used in Maxent software (Phillips, 2008). We created a distance raster using the Euclidean distance tool that measured the distance of each pixel to the forest edge. Distances to the nearest river, settlement, cultivated land area, and road were also extracted using the same tool. Values for the other environmental variables were automatically extracted from the raster at each location of deer occurrence. For any predicting Maxent, all rasters were resampled to a 100-m grid cell size and a mask layer was created from the park boundaries to restrict analysis to both study areas (Young et al., 2011).

Using many correlated variables may result in over-parameterization and reduce the predictive power and interpretability (Morueta-Holme et al., 2010). Multicollinearity was checked for all combinations of environmental variables using Pearson's correlation coefficient. There were strong negative correlations ($R^2 \geq 0.7$) between elevation, rainfall during the driest month and the maximum temperature of the warmest month; elevation, rainfall during the wettest month and minimum temperature of the coldest month. There were strong positive correlations between the maximum temperature of the warmest month, minimum temperature of the coldest month and annual mean temperature; rainfall of the wettest month, rainfall of the driest month and annual rainfall (Appendices 2A, 2B). Thus, only elevation, annual mean temperature and annual mean rainfall were considered in the model. Predictors used in the final model included one categorical variable (NDVI), and 10 continuous variables (elevation, slope, distance to river, distance to primary forest, distance to secondary forest, distance to settlement, distance to cultivated area, distance to road, annual rainfall and annual mean temperature).

We modelled the distribution of each deer species using Maxent v.3.3.3k (http://www.cs.princeton.edu/schapire/maxent/). Maxent is a learning program that estimates the probability distribution for a species' occurrence based on environmental constraints (Phillips et al., 2006). It requires only species presence data and environmental layers (continuous or categorical variables) for the study area. The environmental layers consisted of all environmental variables, as well as a spatial mask layer that restricted the analysis to BINR-WS and UKNP (for more details see Phillips, 2008). We used the following settings of Maxent v.3.3.3k: automatic feature selection, regularization multiplier at unity, maximum of 500 iterations, 50 replicates and a convergence threshold 10−5. The output was in the logistic format for all analyses and the program was run with "auto features" checked (Phillips and Dudik, 2008).

Accuracy assessment for each model was measured by the area under the curve (AUC) from the receiver operating characteristic curve (ROC, Woodward, 1999). The ROC curve is the relationship between the sensitivity and the false positive fraction. The AUC is the area under the ROC curve, with a value of 0.5 representing a random model, values between 0.8 and 0.9 representing models with a good fit and values over 0.9 being an excellent fit (Manel et al., 2001; Thuiller et al., 2003). We also developed distribution map of red muntjac in 2013 and 2014 using presence data from January to April for the wet season and May to July 2013 and 2014 for the dry season.

2.3.3. Variable contribution and response curve

There are two methods to assess the contributions of environmental variables to models: 1) relative contribution and permutation importance and 2) Jackknife test (Phillips and Dudik, 2008). The relative contribution and the permutation importance of each variable were calculated in Maxent as an average over 50 replicate runs. Values were normalized to give the total percent contribution. To get alternative estimates of variable importance, we also ran a Jackknife test. This test generates a model with each variable separately and also creates another set of models, which excludes one of the variables.

3. Results

We recorded 118 photographs of Bawean deer, 6 in the wet season (PER = 0.33) and 112 in the dry season (PER = 3.04), and 4363 photographs of red muntjac, 1614 in wet season (PER = 4.96) and 2749 in dry season (PER = 9.22). Differences between seasons were significant for both species (Bawean deer: $\chi^2 = 41.80$, df = 1, $p < 0.001$; red muntjac: $\chi^2 = 658.15$, df = 1, $p < 0.001$). These differences and the number of data will condition seasonal analyses that will be restricted to the dry season for Bawean deer.

3.1. Habitat use

Bawean deer and red muntjac were found in all sampled habitats, although they were recorded in 8 of the 20 sampled grids and in 156 of the 329 sampled grids, respectively.

Bawean deer encounter rate differed among habitat types in the dry season (H = 7.80, df = 3, p = 0.050). The highest encounter rates were recorded in secondary forest and the lowest in teak forest and shrub (Fig. 2A). Most of camera traps in primary forest did not photograph any deer.

Red muntjac encounter rates differed among habitat types in both seasons: dry H = 68.16, df = 3, $p < 0.001$; wet H = 60.50, df = 3, $p < 0.001$. The highest encounter rates were also recorded in secondary forest (Fig. 2B and C) and differed significantly from all other habitats in both seasons (dry mean rank = 223.4, wet mean rank = 227.7). The lowest encounter rates were recorded in mangrove-swamp (dry mean rank = 126.4, wet mean rank = 111.0) but they did not differ from encounter rates in primary forest (dry mean rank = 141.0, wet mean rank = 147.9). Encounter rates in beach forest did not differ from the former ones in dry season only (dry mean rank = 162.5, wet mean rank = 158.6).

3.2. Species distribution modelling and validation

Distribution models for both species and seasons performed well except for Bawean deer in wet season, when recorded data were scarce. All AUC values were greater than 0.796 (Table 2; Appendix 3). Models identified areas of high probability of presence within both study sites. For Bawean deer in dry season, areas of high predicted suitable conditions are located in the western and central part of the protected area (Fig. 3A). For red muntjac, high probability of suitable conditions included almost the whole area of the park, except the high mountain at the southwest in both seasons (Fig. 3B and C). Red muntjac occupied the same environmental system in consecutive years, either on wet season (Fig. 4A and B) or on dry season (Fig. 4C and D).

3.3. Significant explanatory variables

For Bawean deer, distance to cultivated area had the most relative contribution followed by distance to settlement (56.0% and 24.4%, respectively, Table 3). Based on permutation importance distance to settlement was the most significant variable (42.5%) followed by distance to cultivated area (17.8%), both variables had a

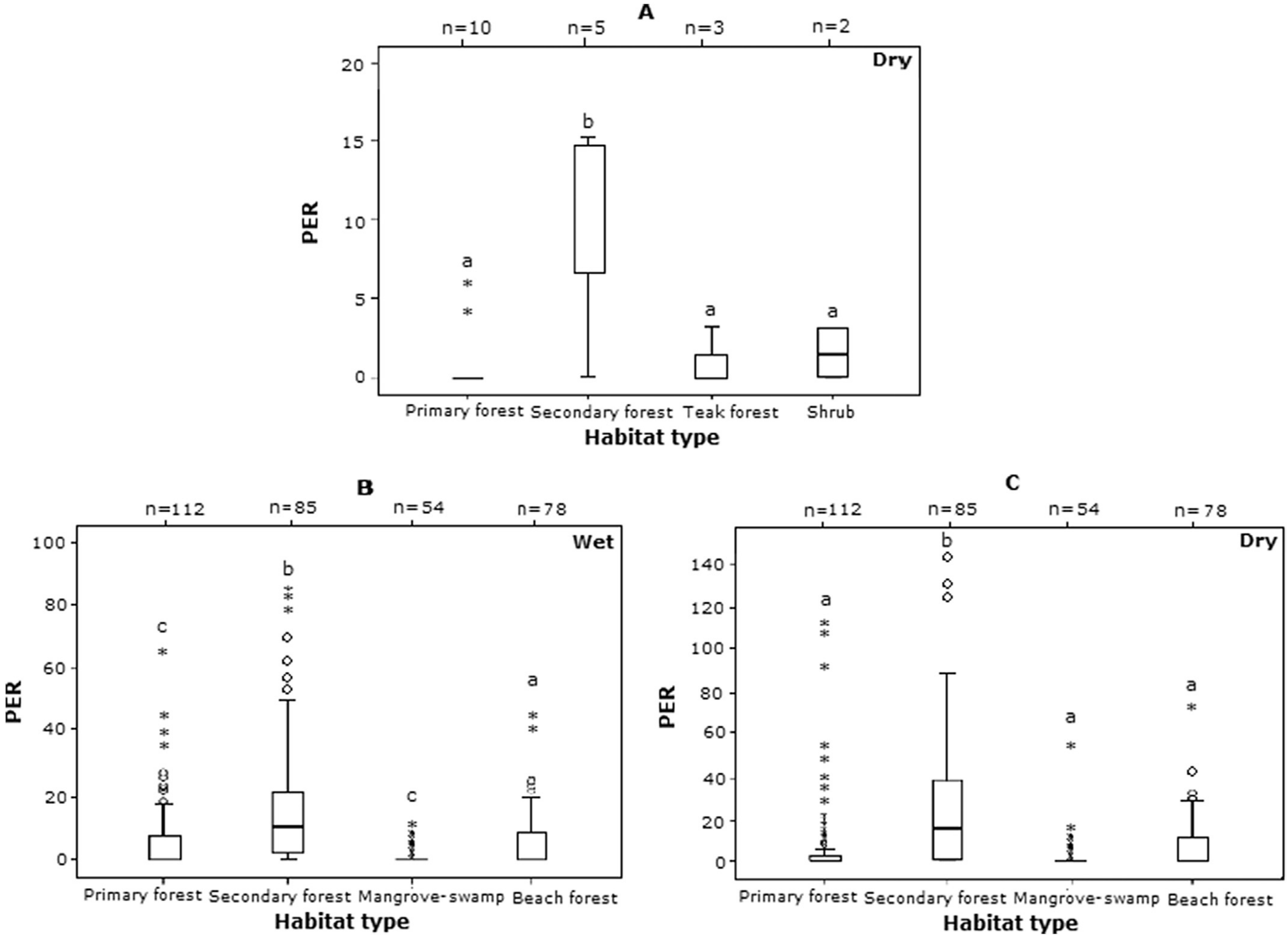

Fig. 2. Photographic encounter rates recorded by camera traps in each habitat type in different seasons, from May to October 2014, in Bawean Island Nature Reserve and Wildlife Sanctuary for Bawean deer (A) and from January 2013 to July 2014, in Ujung Kulon National Park for red muntjac (B, C). Different letters indicate significant differences at the 0.05 probability level (with Bonferroni correction), n = number of camera traps.

Table 2
The AUC and standard deviation for each species model in two season at Bawean Island Nature Reserve and Wildlife Sanctuary and Ujung Kulon National Park.

Species	Season	Number of photographs	AUC	Standard deviation
Bawean deer *Axis kuhlii*	Dry	112	0.796	0.204
Red muntjac *Muntiacus muntjac*	Wet	1692	0.844	0.068
	Dry	2711	0.824	0.058

negative influence on deer occurrence. Response curves were logistic for both variables (Appendix 3A). Distance to cultivated area had the greatest relative contribution both in wet and dry seasons for red muntjac, (56.0% and 57.8%, respectively) followed by annual rainfall (19.3% and 18.2%, respectively). Based on permutation importance, distance to cultivated area was the most significant both in wet and dry seasons (50.2% and 49.6%, respectively) followed by elevation (11.1% and 12.9%, respectively). Distance to cultivated area and elevation negatively influenced deer occurrence on the contrary of annual rainfall. Response curves were roughly unimodal for distance to cultivated area and bimodal for annual rainfall in both seasons (Appendix 3B).

Jackknife test in Bawean deer suitability model showed the highest gain when “distance to cultivated area” was used alone, while “distance to secondary forest edge” most increased the gain when it was omitted (Fig. 5A). Jackknife tests in red muntjac suitability models showed the highest gain when “distance to cultivated area” was used alone (Fig. 5B and C).

4. Discussion

Although this study likely represents the largest camera trapping dataset for Bawean deer and red muntjac, the number of photographs was fairly low for Bawean deer in the most favourable areas of the range. This is reflective of the rarity of this species and echoes its current status of “critically endangered” (Semiadi et al., 2013). In a previous camera trapping study, UGM. and BBKSDA East Java (2004) did not record any photograph of Bawean deer inside BINR-WS, even during the dry season (September to October). The number of photographs was lower in the wet season

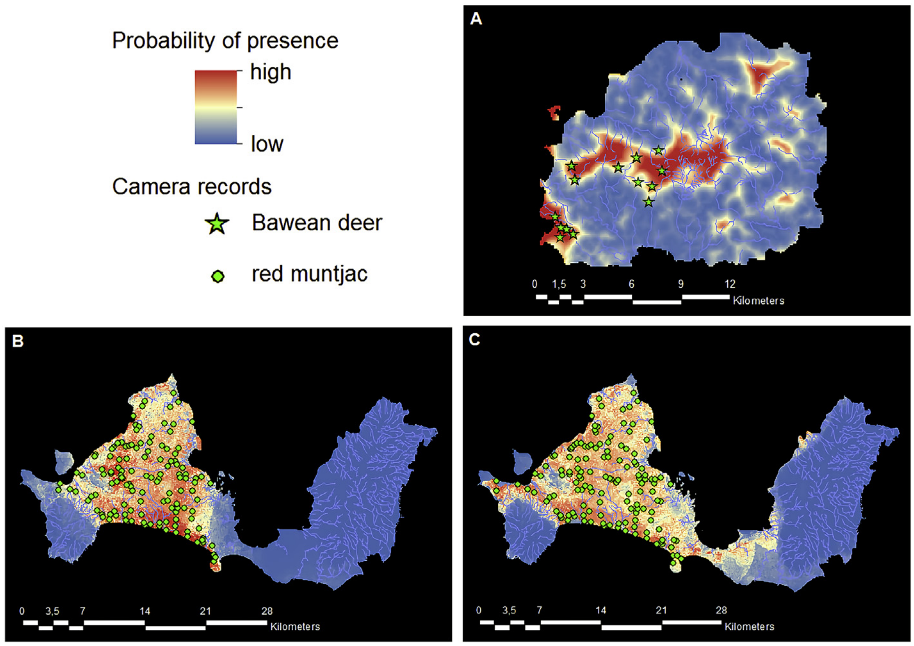

Fig. 3. Distribution map of (A) Bawean deer in the dry season and (B, C) red muntjac in the wet and dry seasons respectively.

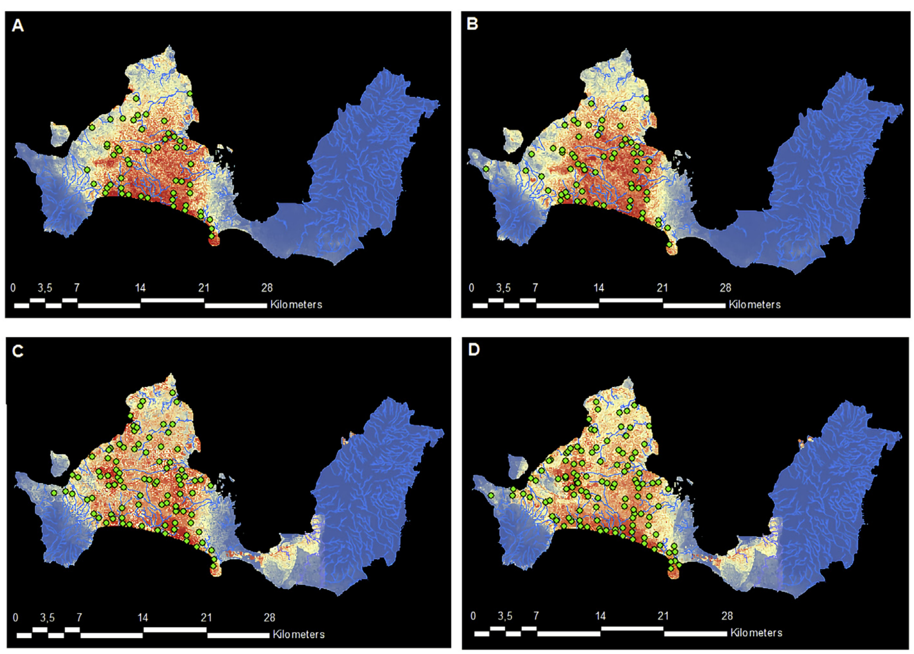

Fig. 4. Distribution map of red muntjac in the wet season (A - 2013, B - 2014) and the dry season (C - 2013, D - 2014). See legend of colors in Fig. 3.

for both species, possibly related to a lower level of activity or more probably to a greater availability of food. It is known that the time dedicated by animals for searching and obtaining food is inversely proportional to its abundance (Chappell, 1980). In most tropic habitats, food availability is assumed to be uniform throughout the year (Foster, 1973; Frankie et al., 1974), but can become scarcer during the dry season (Pontes and Chivers, 2007), leading to broader movements and higher probability of encounter with a camera trap (Rahman et al., 2016).

The hypothesis that both deer species mostly use areas with primary forest-type was not supported by our results. More than 50% of Bawean deer and red muntjac were detected in secondary forest, which cover respectively 25.0 and 25.8% of the grids and are mainly located at low elevation in both study sites. Although Teng et al. (2004) suggested that deer of the genus *Muntiacus* are habitat generalists, including varied elevations, Steinmetz et al. (2008) found that signs, and presumably *Muntiacus vaginalis*, were significantly more common in lower than higher-lying areas of the Tenasserim-Dawna mountains, Thailand.

The encounter rate was significantly higher in secondary forest than in all other habitat types for both species. Blouch and Atmosoedirdjo (1987) also found that Bawean deer was

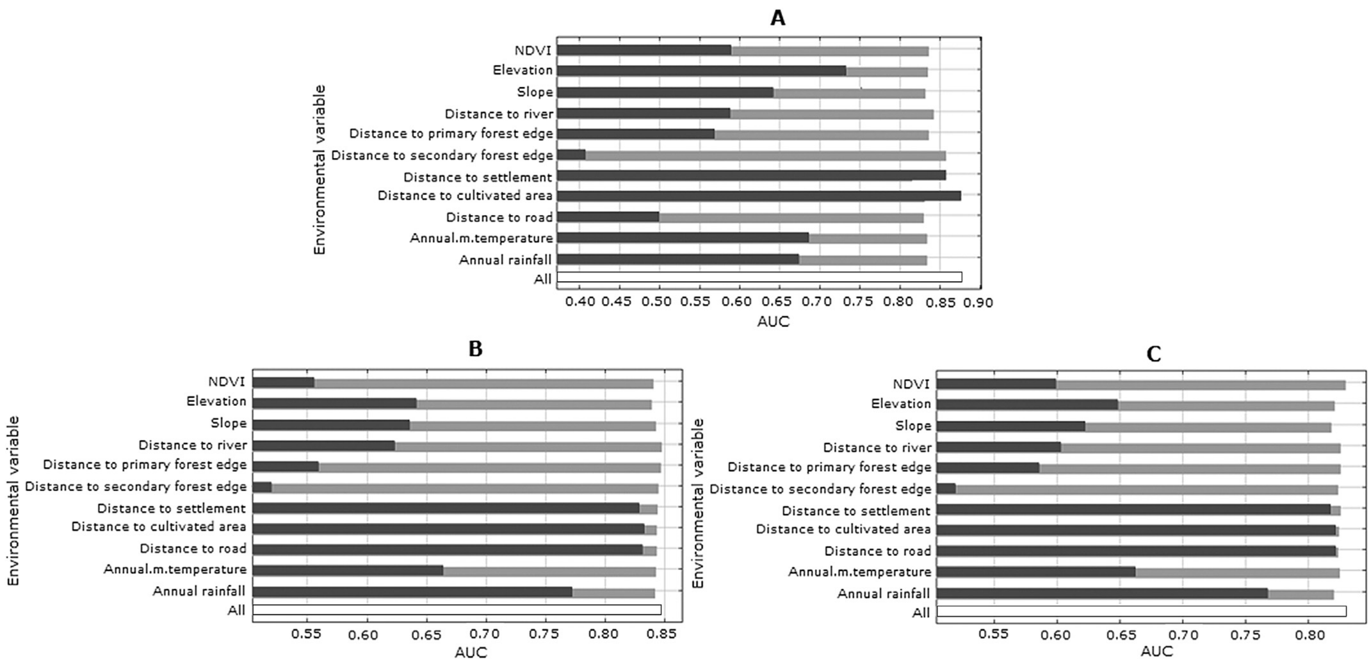

Fig. 5. Jackknife tests of AUC values of the Maxent models applied to Bawean deer in the dry season (A) and to red muntjac in the wet (B) and the dry (C) seasons. For each variable, the black bar corresponds to the model generated with this variable alone; the light grey bar corresponds to the model generated without this variable. The white bar corresponds to the model generated with all variables.

Table 3
The relative contribution (RC) and permutation importance (PI) of each environmental variable for each species as an average over the 50 replicates. Values are normalized to give percentages.

Environmental variable	Bawean deer		Red muntjac			
	Dry season		Wet season		Dry season	
	RC	PI	RC	PI	RC	PI
NDVI	5.9	4.7	5.5	6.1	2.3	1.7
Elevation	1.7	1.3	7.7	**11.1**	6.5	**12.9**
Slope	0.1	0.2	2.6	3.8	2.6	2.8
Distance to nearest river	2.8	6.6	0.3	1.5	0.5	3.4
Distance to primary forest edge	5.9	4.7	0.1	0.1	0.1	1.3
Distance to secondary forest edge	0.6	1.6	0.1	0.3	0.3	0.3
Distance to nearest settlement	**24.4**	**42.5**	0.5	7.0	7.1	4.7
Distance to nearest cultivated area	**56.0**	**17.8**	**56.0**	**50.2**	**57.8**	**49.6**
Distance to nearest road	1.2	8.8	6.7	8.8	3.6	9.9
Annual mean temperature	0	0	1.1	6.2	0.9	7.7
Annual rainfall	1.6	11.8	**19.3**	4.8	**18.2**	5.7

The environmental variables mattered most and determine to both of deer occurrence.

significantly more recorded in secondary forest than in three of four other habitat types. According to Brown and Lugo (1990) secondary forests have higher productivity than primary ecosystems. Ground cover in the secondary forest habitat is relatively sparse and dominated mostly by fruit trees canopy in both of study sites. This structure may be conducive to Bawean deer and red muntjac, which routinely forages on fruits, buds, tender leaves, flowers, herbs and young grass (Blouch and Atmosoedirdjo, 1987; Kitchener et al., 1990; Oka, 1998). Indeed, most animals were photographed when feeding. In UKNP fruits of sugar palms, *Arenga obtusifolia,* offer an abundant source of food for muntjac, a high consumption of these fruits was recorded on photographs. On the contrary, previous studies (Supriatin, 2000; Santosa et al., 2013) indicate that the dominance of this rapidly spreading palm species reduces the availability of food plants for rhinos.

Encounter rates in primary forest was higher than in teak forest and shrub for Bawean deer, and lower than in beach forest for red muntjac. The food offered by this habitat to deer species seems good but is scarcer than in secondary forest (Blouch and Atmosoedirdjo, 1987; Parry et al., 2007; García-Marmolejo et al., 2015). Nevertheless, it is likely that both deer require nearby areas of primary forest as refuge for resting (Blouch and Atmosoedirdjo, 1987; Seagle, 2003). Teak forest of BINR-WS regularly burns naturally in dry season and a brushy understory of grasses and small shrubs develops, offering food at certain periods to Bawean deer.

Presence of red muntjac in beach forest may be related with food and mineral requirements. Mineral licks have long been recognized as areas to which wild animals, particularly ungulates, are attracted (Schultz and Johnson, 1992; Montenegro, 2004; Ayotte et al., 2008; Poole et al., 2010; Matsubayashi and Lagan, 2014). As an example, sodium (Na), which is available in large quantities on vegetation around the beach, is the mineral most sought by white-tailed deer when using mineral licks (Kennedy et al., 1995).

Low encounter rates of Bawean deer in shrub and red muntjac in mangrove-swamp were expected because food is scarce, and also because the cover, although dense, is usually too hot during the day to be comfortable for deer (Blouch and Atmosoedirdjo, 1987).

According to our Maxent models the distribution of red muntjac did not differ between seasons even if, as well as for Bawean deer, the number of photographs was lower in the wet season. Both species selected mostly forests far from cultivated areas. Many studies on ungulate species already reported the influence of human infrastructures and activity on habitat use (e.g. Wolfe et al., 2000; Nellemann et al., 2001; Setsaas et al., 2007). However, red muntjac occur in plantations of coffee, rubber, sugarcane, cassava, coconut and teak adjacent to forest (Laidlaw, 2000; Azlan, 2006), and may also benefit from agricultural conversion at forest edge (M. Tysoon pers. comm.). More, Bawean deer were recorded in fields bordering forests by night where they ate young leaves of corn and cassava particularly in the dry season, retreating to relatively safer habitats during daytime (Semiadi, 2004). Habitat use can also be associated with relatively safer habitats from predator risk (Arceo et al., 2005). Indeed ungulates seem to be able to tolerate human activity to a higher extent during periods of food shortage (Strand et al., 2006). It seems cultivated areas affect both of deer in two ways. First, reduce and isolate the amount of natural habitat so that all that remains in heavily farmed areas are scattered remnant patches, and linear strips awash in a sea of cropland. Second, agroecosystem itself is a simplified, which continues restless environment that replaces a richer natural diversity with relatively poor collection of cultivated plants and domesticated animals and may add a small amount of additional food.

The impact of human settlements is highly significant for Bawean deer and not for red muntjac. Bawean deer were not recorded closer than 2500 m to the nearest settlement. This is likely the result of avoiding human disturbance and feral dog conflicts, as part of an anti-predator behaviour that increased travel costs to move away from disturbance (Formaniwicz and Bobka, 1988), and perhaps more importantly, reduced opportunity to forage in optimal habitat when humans are most active (Creel et al., 2005). For Bawean deer in the absence of natural predators, humans and feral dogs could affect their habitat use. Indeed, agricultural crops place Bawean deer at risk from feral dogs (Blouch and Atmosoedirdjo, 1987). So, no feral dog was recorded by six over the nine camera traps where Bawean deer were detected, when dogs were photographed by 12 camera traps over 20 (Rahman et al., 2016). Moreover, we have been informed of two cases of Bawean deer killed by feral dogs close to settlements.

Based on the distribution map, red muntjac were mostly located near crop lands, particularly in the dry season. This flexible species which is known to live sometimes in such habitat close to the forest edge (Mattioli, 2011) likely responds more to the availability of food than to tolerance to human disturbance.

The influence of annual rainfall on habitat use by red muntjac only could be related to habitat availability. This deer was more recorded in the south than in the north of UKNP, namely where rainfall is the highest (3000–3500 mm/year) and habitat dominated by secondary and primary forests. These are the main biotopes of red muntjac (Mattioli, 2011), unlike the mangrove forests which dominate in the north of the park. Conversely, in BINR-WS rainfall is almost uniform over the island and is not related to any habitat type. Temperature did not significantly affect the distribution of deer which is not surprising given the small differences in mean monthly temperatures in both sites (17–32 °C in BINR-WS, 17–30 °C in UKNP). Moreover, both deer tend to live in areas where the range of temperature is smaller, 22–26 °C for Bawean deer, 21–25 °C for red muntjac according to http://landsat.usgs.gov. However this variable could become relevant in the scope of the global as small changes in temperature can have drastic effects on tropical species and thus on their distribution patterns (IPCC, 2007a; Wright et al., 2009, 2010). Other variables such as elevation, slope, NDVI, distances to secondary forest and to road were not significant, likely because their variation were too small in both sites and/or fall within the usual range for the species. This is the case with elevation and slope in UKNP for red muntjac which can reach 800 m in Java (S. Hedges, pers. comm.). The positive influence of NDVI suggested that both species prefer forest to open areas but, with ca. 70% of all forest habitat types in the areas, secondary forests were highly dominant and always close for deer. Although roads infer human disturbance for both deer, distance to road was not significant. This could result from a trade-off between sense risk and movement ease in fragmented habitat, particularly for Bawean deer which can travel long distances in the dry season (Blouch and Atmosoedirdjo, 1987). In our study Bawean deer locations were closer to urban and cultivated area, where road connected forest patches. This should be investigated further by setting cameras along roads.

5. Conclusion

Our study revealed the prevalence of Bawean deer and red muntjac in secondary forest versus other habitat types. Both species can use habitats at the edge of forest where they are at greater risk of conflict with humans, using forest as a refuge and exploiting agricultural landscapes for getting additional food (Blouch and Atmosoedirdjo, 1987; O'Brien et al., 2003). This highlights the importance of protected areas. Up to now, conservation initiatives for deer have been extremely limited in Indonesia due to a lack of knowledge on the ecology of these species, particularly for Bawean deer. Both deer received little conservation attention, mainly because they are uncommon, rarely seen, and locally compete for conservation interest with more charismatic species such as Sumatran tiger *Panthera tigris sumatrae* (Pocock, 1929), Sumatran elephant *Elephas maximus sumatranus* (Temminck, 1847) or Javan rhino.

Habitat degradation and loss are ongoing threats to deer in Indonesia. Protected areas have become islands of habitat within a mosaic of agriculture and urbanization, and they suffer illegal logging and deforestation (Meijaard et al., 2005). With an appropriate degree of caution, we feel that our results are a basis of knowledge for other areas and are essential for implementing conservation initiatives including identifying areas of conservation priority, developing anti-poaching efforts, and even initiating anti-encroachment operations.

Authors' contributions

All author conceived and designed this study. DAR, MH, AM, and AYF performed the field work, collected the field data. DAR analyzed the camera trap data. DAR, GG and SA wrote the manuscript. After reading the final manuscript carefully, all the authors approved it.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2017.05.008.

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