POPULATION ECOLOGY – ORIGINAL RESEARCH



Biotic and abiotic drivers of dispersion dynamics in a large-bodied tropical vertebrate, the Western Bornean orangutan

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Abstract

Understanding of animal responses to dynamic resource landscapes is based largely on research on temperate species with small body sizes and fast life histories. We studied a large, tropical mammal with an extremely slow life history, the Western Bornean orangutan (*Pongo pygmaeus wurmbii*), across a heterogeneous natural landscape encompassing seven distinct forest types. Our goals were to characterize fluctuations in abundance, test hypotheses regarding the relationship between dispersion dynamics and resource availability, and evaluate how movement patterns are influenced by abiotic conditions. We surveyed abundance in Gunung Palung National Park, West Kalimantan, Indonesia, for 99 consecutive months and simultaneously recorded weather data and assessed fruit availability. We developed a Bayesian hierarchical distance sampling model to estimate population dispersion and assess the roles of fruit availability, rainfall, and temperature in driving movement patterns across this heterogeneous landscape. Orangutan abundance varied dramatically over space and time. Each forest type was important in sustaining more than 40% of the total orangutans on site during at least one month, as animals moved to track asynchronies in fruiting phenology. We conclude that landscape-level movements buffer orangutans against fruit scarcity, peat swamps are crucial fallback habitats, and orangutans' use of high elevation forests is strongly dependent on abiotic conditions. Our results show that orangutans can periodically occupy putative-sink habitats and be virtually absent for extended periods from habitats that are vitally important in sustaining their population, highlighting the need for long-term studies and potential risks in interpreting occurrence or abundance measures as indicators of habitat importance.

Keywords Bayesian hierarchical distance sampling · Habitat shifts · Occupancy · Population dispersion · Tropical ecology

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Introduction

Ecologists have long been interested in how animals persist on landscapes in which the availability of resources varies dramatically across space and over time (Charnov et al. 1976; Rosenzweig 1991). Research on this topic has led to the development of foundational ecological theory, such as source–sink models that predict population dynamics in landscapes comprising habitats of differing quality (Pulliam 1988). There has also been substantial effort spent on understanding how animals move across heterogeneous landscapes to meet their fundamental fitness requirements (e.g., foraging, avoiding predation, maintaining body temperature; Altmann 1974; McPeek and Holt 1992; Boyce et al. 2002; Avgar et al. 2013).

Currently, however, there are two important shortfalls in ecological studies investigating the responses of animal populations to dynamic resource landscapes. First, research has primarily focused on small-bodied species with fast life histories (e.g., mammals: Kelt et al. 2019; Presley et al. 2019), whose responses to spatiotemporal variation in habitat quality may be qualitatively different from species with larger body sizes or slower life histories. For example, larger-bodied, longer-lived species generally travel further, subsist on lower quality foods, have lower basal metabolic rates, possess greater behavioral plasticity, and exhibit longer periods of juvenile development with enhanced opportunities for learning (Brockman and van Schaik 2005). These qualities may permit a wider range of responses to challenging environmental conditions. Second, studies investigating the effects of habitat heterogeneity on the distribution, abundance, and movement patterns of animal populations have been disproportionally conducted in temperate regions (e.g., Presley et al. 2019). Patterns of spatiotemporal variation in environmental conditions in temperate regions can differ substantially from other regions, such as the tropics which contain the majority of the world's animal species. Pronounced inter-annual variability in biotic and abiotic conditions (e.g., Karr and Freemark 1983; Shine and Brown 2008) and plant phenology (Wich and van Schaik 2000; Cannon et al. 2007a, b) in tropical regions likely create challenges not encountered by animals in temperate systems that exhibit more predictable seasonality. Thus, studies of large-bodied, tropical species with slow life histories may meaningfully contribute to our broader understanding of how animals respond to spatiotemporal change in habitat quality.

Researchers examining how animals distribute themselves in response to changes in the spatial and temporal availability of key resources frequently employ landscape use models. These models attempt to quantify how specific environmental variables (e.g., vegetation types) influence the distribution of individuals across heterogeneous landscapes. A variety of modeling approaches for different types of data are currently employed to characterize landscape use (reviewed in Wisdom et al. 2020). Among the most common are resource selection functions (RSFs) typically derived from high-resolution location data from telemetered individuals (Boyce et al. 2002; Manly et al. 2002). RSFs compare multiple environmental measures assessed at both known animal locations and random points to identify reliable correlates of habitat use. The identified correlates are rarely directly tied to habitat use by focal individuals however, and as such linking results from RSFs to life history characteristics or population abundance is challenging (Boyce et al. 2016; Mason and Fortin 2017). Furthermore, population-level inferences based on studies of telemetered individuals are limited by high costs and resultant small sample sizes. Recent methodological advances, such as hierarchical distance sampling models (Kéry and Royle 2016) that account for imperfect detection and variation in sampling effort, offer new, lower-cost opportunities to both detect spatiotemporal fluctuations in abundance and link observed fluctuations to variability of important resources.

The survival of individual animals depends on their ability to effectively allocate time among the different parts of their home range (Altmann 1974). In landscapes where resource availability or risk exposure varies dramatically across space and over time, the fitness value of a particular portion of the home range is not constant (Altmann 1974). Over time, however, some habitats may be more intensively used (i.e., have higher "area occupation densities" sensu Altmann 1974) than others, reflecting their higher net value to individuals and, ultimately, the population. Identifying such habitats for animals occupying dynamic landscapes would have both theoretical and applied value. Theoretically, assessment of the long-term value of different habitats could inform understanding of many topics of interest to landscape, movement, and population ecologists (e.g., determinants of carrying capacity, source-sink population dynamics). Identification of habitats that are crucial for population persistence can also inform applied questions regarding population management and conservation, particularly in the face of rapid changes in climate and land-use.

Orangutans (*Pongo* spp.) present an excellent opportunity to investigate how spatiotemporal variation in habitat quality influences population dispersion (i.e., the distribution of individuals across the landscape). Orangutans are large, primarily arboreal, tropical vertebrates with slow life histories. They range widely and occupy a diverse array of habitats (Leighton and Leighton 1983; Husson et al. 2009; Singleton and van Schaik 2001). Furthermore, their preferred food resources, ripe fruits, exhibit dramatic variation over space and across time (Buij et al. 2002; Marshall et al., 2009; Kanamori et al. 2017). Despite their iconic status as symbols of rainforest conservation (Clucas et al. 2008; Spehar et al. 2018) and decades of long-term research (Wich et al. 2009), our understanding of orangutan movement dynamics in space and over time is surprisingly limited (Meijaard et al. 2012). More specifically, we know little about how spatiotemporal variation in environmental conditions affect the dispersion of orangutan populations across heterogeneous landscapes (Marshall et al. 2009).

One of the challenges of studying orangutan dispersion is the species' rarity; on Borneo they rarely are found at densities higher than 2–4 individuals km^{-2} (Husson et al. 2009). For this reason, current knowledge about variation in orangutan abundance patterns has largely come from indirect surveys of the nests they build each night (e.g., Buij et al. 2002; Kanamori et al. 2017). Although such surveys can be valuable, there are well-known issues with the accuracy and precision of nest surveys. For example, the amount of time a nest remains visible-a parameter required to convert nest counts to estimates of population density-can vary widely among sites and over time (Mathewson et al. 2008; Marshall and Meijaard 2009). Even when nest decay rates can be accurately estimated, a simulation study suggested that nest surveys produce population estimates that are accurate to within 33% of the true population size only 50% of the time (Boyko and Marshall 2010). Furthermore, because nest counts integrate abundance data over periods of several months or more, they potentially mask more subtle, yet ecologically important patterns, such as responses to rapid fluctuations in environmental conditions. Thus, fine-scaled data based on direct observations of individuals may provide a deeper understanding of orangutan dispersion across heterogeneous landscapes than has previously been possible.

Broadly speaking, heterogeneity in population dispersion either reflects spatial variation in vital rates (e.g., varying population growth rates in response to habitat quality) or movements of groups or individuals among habitats (e.g., tracking spatiotemporal variation in resource availability or predation risk), or some combination of the two (Pulliam 1988; van Moorter et al. 2013; Mason and Fortin 2017). Orangutans have very low rates of mortality and reproduction (Knott 2001; van Noordwijk et al. 2018), typically travel and feed alone or solely with dependent offspring (Mitra Setia et al. 2009), and are known to move substantial distances in search of fruit (Singleton and van Schaik 2001). Therefore, variation in orangutan dispersion largely reflects the cumulative effects of individual decisions about when and where to move across the heterogeneous landscape, rather than spatial variation in birth or death rates.

We monitored the distribution and abundance of a population of orangutans, *P. pygmaeus wurmbii*, in Western Borneo for more than eight years using direct observations along transects spread across a wide gradient of natural forest types and elevation. We simultaneously sampled the productivity of each forest type using botanical plots and collated temperature and rainfall data from 14 weather stations located across the habitat gradient. Using a hierarchical distance sampling model, we estimated orangutan abundance and evaluated how temporal variations in orangutan dispersion were related to ecological predictors. We sought to test the following two (non-mutually exclusive) hypotheses:

H1. Orangutan dispersion dynamics are a consequence of movements that buffer individuals against local fruit scarcity

Heterogeneous landscapes are commonly thought to promote population stability, in part because they provide a diversity of resources that can act as 'insurance' against ecological extremes (Oliver et al. 2010). Orangutan population densities tend to be higher at sites in which individuals have access to multiple forest types than at homogenous sites (Husson et al. 2009) and orangutans also extend their home ranges whenever possible to included phenologically or floristically distinct habitats (Singleton and van Schaik, 2001), suggesting that habitat heterogeneity plays an important role in this taxon. Specifically, individual orangutans are hypothesized to move among distinct forest types to track spatiotemporal variation in fruit availability (Buij et al. 2002, Sugardjito et al. 1987, te Boekhorst et al. 1990). Our combination of direct observations, a long study duration, and frequent sampling across a wide range of habitats provides a strong test of this hypothesis, and allowed us to consider additional nuanced questions. For example, we were able to examine whether orangutan habitat use is primarily driven by preference for areas with high fruit productivity or avoidance of areas with low fruit productivity, and identify important habitats that may be disproportionately important in supporting orangutans long-term (Marshall 2018).

H2. Orangutan dispersion dynamics reflect the effects of abiotic conditions on orangutan movement patterns

Species distribution models are widely used to project the future availability of habitat for tropical vertebrates, including orangutans (Gregory et al. 2012; Struebig et al. 2015a). Abiotic conditions—specifically temperature and rainfall–figure prominently in these models. For example, using coarse-grained orangutan occurrence records from across Borneo, Struebig et. al. (2015a) found that the best environmental parameters for predicting orangutan habitat suitability included measures of temperature and rainfall. Gregory et al. (2012) found that temperature had a moderately positive effect on orangutan nest presence in Sabah, Malaysia, although it was a less important predictor than measures of degradation, distance from roads, or forest cover. These results suggest that abiotic conditions are important determinants of orangutan occurrence patterns at large spatial scales, although to date the effects of weather on orangutan habitat use and abundance on fine scales are poorly understood. We thus examined the effects of rainfall and minimum and maximum temperature on orangutan habitat use across a wide range of natural forest types along an elevational gradient, allowing us to assess whether the effects of abiotic conditions might be mediated by habitat type.

Material and methods

Study site

We collected data at the Cabang Panti Research Station in Gunung Palung National Park, West Kalimantan, Indonesia (1°13' S, 110°7' E, Fig. 1). The site encompasses approximately 34 km² and comprises seven distinct, contiguous forest types that differ in underlying geology, soil type, drainage, elevation, plant species composition, forest structure, and plant phenology: (1) *peat swamp forest* on nutrient-poor, sandy soils covered by a layer of organic matter (5–10 m asl); (2) *freshwater swamp forest* on nutrient rich,



Fig. 1 Study site. Top panel depicts the trail system (black lines) at the Cabang Panti Research Station. Rivers are indicated in blue and the seven forest types are differentiated by color; habitat type colors are consistent across all figures. The numbers across the top indicate rough elevation (in meters above sea level) of the contour line separating the adjacent forest types (although habitat boundaries only

loosely follow elevational contours). The bottom panels show, from left to right, contour lines of the area inside and surrounding the trail system, the location of the study site within Gunung Palung National Park, the park's location in West Kalimantan, and the location of West Kalimantan on Borneo periodically flooded, and poorly drained gleyic soils (5-10 m asl); (3) alluvial bench forest on fertile sandstone-derived soils near rivers (5-100 m asl); (4) lowland sandstone forest on well-drained soils derived from sandstone parent rock (20-200 m asl); (5) lowland granite forest on well-drained, granite-derived soils (200-400 m asl); (6) upland granite forest on well-drained, granite-derived soils (350-800 m asl); and (7) montane forest on largely granite-derived soils (750–1100 m asl; Marshall 2009; Marshall et al. 2014). Boundaries among forest types are distinct and clearly discernable in the field. Each forest type inside the research area is contiguous with and representative of much larger areas of each forest type outside the trail system (Fig. 1). Therefore, the results of our focused sampling within the research area can be scaled up to represent patterns across the much larger landscape. Because Borneo is devoid of natural predators large enough to pose a serious risk to adult orangutans, per capita resource availability or abiotic factors, not predation, are likely the primary ecological determinants of individual movement decisions. We note, however, that socio-ecological factors not measured in this study likely are also important. Some of these, such as female-female feeding competition (Knott et al. 2008) are likely tied to per capita resource availability, but others, such as seeking mates or avoiding sexual coercion, may be only loosely tied to food abundance (te Boekhorst et al. 1990).

Orangutan transects

We sampled orangutans on a series of fourteen survey transects across the seven forest types at Cabang Panti from October 2007 through December 2015. Survey transects were approximately 3.5 km in length and followed small foot trails through the forest. We walked each of the transects twice per month (starting at opposite ends) at the same speed and time of day (beginning at 05:30 h), and gathered standard line transect data for all orangutans encountered (e.g., perpendicular sighting distance, number of individuals sighted; Buckland et al. 2001). Orangutans were detected either by sight or sound. If we heard a sound (e.g., vocalization, dropped fruit) that may have indicated the presence of an orangutan, we temporarily left the transect to visually determine whether an orangutan was present. Thus, all encounters were visual, although often we were first alerted to orangutan presence through sound. Some orangutans in the lowlands are well habituated to human observation due to the presence of a long-term orangutan research project on site (Knott et al. 2008). Less than 1% of our observations comprised orangutans currently being followed by other researchers, however, and in these rare instances animals were typically detected prior to the human observers. Orangutans at higher elevations were unhabituated, although they still had the opportunity to see people, as researchers

regularly visited all forest types to collect ecological data. The consistent, slow, systematic searching for orangutans on all transects by skilled observers suggest that their level of habituation did not introduce bias. Over our study period, we surveyed 8666.5 km of transects and observed orangutans 695 times during 413 independent encounters that included groups of multiple adult orangutans and mother–offspring pairs. Mean sampling effort was 12.6 km (2.9 SD) per forest type per month.

Weather data

We collected weather data (min temperature, max temperature, and rainfall) daily at the field station during the sampling period; the station is located at 25 m asl in alluvial bench forest. In addition, we placed two weather stations in each of the seven forest types (in the upland habitats one station was placed on each of the two ridges in the study site) and used them to monitor min–max temperature and cumulative rainfall weekly. We measured temperature using Taylor analog dual-reading min–max thermometers and rainfall with Forestry Suppliers metric rain gauges with large capacity overflow chambers.

Phenology plots

We monitored 10 randomly placed botanical plots in each of the seven forest types. Three of the peat swamp plots were in an isolated patch of heath-like peat surrounded by alluvial bench and freshwater swamp forest (see Fig. 1) in which there were no vertebrate transects. We thus excluded them from this analysis and present data from the remaining 67 plots. Plots were either 0.1 or 0.2 ha in size; there were five of each in each forest type, resulting in 1.5 ha of plots sampled per month per forest type (except the peat swamp, where only 1.0 ha was sampled monthly). In each plot, all trees larger than 14.5 cm DBH, all lianas larger than 3.5 cm DBH, and all hemi-epiphytic figs whose roots reach the ground were identified, measured, and tagged (Marshall 2009). We used the 14.5 cm (rather than 15 cm) DBH cutoff for trees to ensure equal bin widths for all included sizes when rounding (e.g., 14.50-15.49, 15.50-16.49. A cut-off at 15 cm DBH would have resulted in 50% fewer trees that could possibly be measured at 15 cm than any subsequent size. Similarly, as our long-term data collection on lianas suggests most taxa reach reproductive maturity at or above 4 cm DBH, we used 3.5 cm as the cut-off. Each month we assessed each tagged tree, fig, and liana stem and assigned it to one of six reproductive states: reproductively inactive, bearing flower buds, flowers, immature, mature, or ripe fruits (Cannon et al. 2007b). Due to funding constraints, we only monitored phenology in montane forests between October 2007 and August 2011; all other plots were monitored for the full study period. Sample sizes of stems were consistent across the study period with the exception of stems that died or stems that recruited into the monitored size class during the research period.

Because orangutans preferentially feed on mature and ripe fruits (Leighton 1993), we used the total number of stems per hectare in these two phenological states as a monthly index of fruit availability. We did not restrict our phenology data collection to only stems known to be fed upon by orangutans because the vast majority of behavioral data collected on orangutans at our site has been collected in the lowlands. Including only trees observed to have been fed upon in the lowlands would potentially bias against fruit availability measures at higher altitudes, where orangutans may feed on taxa that they normally avoid (e.g., Calophyllum) or are not available (e.g., montane Agathis) at lower elevations (see discussion in Marshall et al. 2009). We acknowledge, however, that basing our phenology measure on all plant stems likely led to the inclusion of some stems that orangutans do not consume.

Data analysis

We used a hierarchical distance sampling model (Kéry and Royle 2016) to estimate orangutan abundance. We estimated abundance based on counts of orangutans (accounting for imperfect detection) and perpendicular sighting distances between observed orangutans and the transect line (Buckland et al., 2001). We estimated detection probability using the half normal distribution: $g(x) = \exp\left(-\frac{x^2}{2\sigma_{ij}^2}\right)$, where *x* is the perpendicular sighting distance, and σ_{tj} is the scale parameter at each sampling period *t* at transect *j*. We accounted for changes in sampling effort by offsetting σ_{tj} . We binned each observed distance into 10 m wide classes, and calculated detection probability, p_{tj} , using a multinomial process (Kéry and Royle 2016).

The observed number of orangutans, n_{ij} , at each sampling period t and transect j was distributed as a binomial distribution: $n_{ij} \sim \text{Binomial}(N_{ij}, p_{ij})$, where N_{ij} is the true latent abundance and p_{ij} is the detection probability. Latent abundance, N_{ij} , was modeled using a zero-inflated Poisson distribution: $N_{ij} \sim \text{Poisson}(\tilde{\lambda}_{ij})$, with mean $\tilde{\lambda}_{ij} = \lambda_{ij} \cdot z_{ij}$ in which z_{ij} is a Bernoulli random variable to account for excess zeros. We derived orangutan density, D_{ij} , by dividing N_{ij} , the latent abundance, by A_i , the area of each transect.

We modeled expected abundance, λ_{ij} , with a log-link function and covariates:

$$\log(\lambda_{tj}) = \alpha_{k(j)} + \beta_{F,k(j)} \times \operatorname{Fruit}_{tj} + \beta_{R,k(j)} \times \operatorname{Rain}_{tj} + \beta_{H,k(j)}$$
$$\times \operatorname{High}_{tj} + \beta_{L,k(j)} \times \operatorname{Low}_{tj} + \varphi_j + \gamma_t + \log(\operatorname{offset}_j).$$

Here, $\alpha_{k(i)}$ is the forest type-specific intercept for k = 1, ... 7 forest types (see *Study site* section) where k(j)denotes the forest type of each transect j; $\beta_{F,k(j)}$ is the forest type-specific interaction term for the effect of fruit stems, Fruit_{ti}, by each forest type, k(j); $\beta_{R,k(j)}$ is the forest typespecific interaction term for the effect of rainfall, *Rain_{ti}*, by each forest type, k(j); $\beta_{H,k(j)}$ is the forest type-specific interaction term for the effect of maximum temperature, High_{ti}, by each forest type, k(j); $\beta_{L,k(j)}$ is the forest type-specific interaction term for the effect of minimum temperature (Low_{ti}) by each forest type, k(i). Each of the parameters (intercept and effects) were specified as random effects by forest type. For example, the interaction of forest type and fruit stems was drawn from a normal distribution: $\beta_{F,k} \sim \text{Normal}(\mu_F, \sigma_F)$, where μ_F is the fixed effect of fruit stems at the average forest type and σ_F is the standard deviation across forest types. We added random effects for both transect, φ_i , and sampling period, γ_t , to account for spatial and temporal variation. We also accounted for slight variation in transect length by adding in $log(offset_i)$, which is the length of each transect j divided by the average transect length. Covariates were not sufficiently correlated to raise concerns about collinearity (mean correlation among covariates = -0.05, range -0.43to 0.23). All continuous covariates were standardized to have a mean of 0 and a standard deviation of 1 to allow straightforward comparisons of effect sizes. Missing covariate values were interpolated from a normal distribution with mean 0 and standard deviation of 1.

We estimated model parameters using a Bayesian framework in JAGS version 4.2.0 (Plummer 2003) via program R (version 3.4.1; R Core Team 2017) with the JagsUI package (version 1.4.2; Kellner 2016). We used three parallel chains for 120,000 iterations with a burn-in of 100,000 and a thin of 10 for a total of 2,000 draws from the posterior distribution for each parameter. We used uninformative priors for all parameters and the Gelman–Rubin statistic (<1.1) as well as visual inspection to evaluate model convergence.

To examine temporal changes in orangutan dispersion among forest types, for each month we calculated the proportion of the total number of orangutans at the site found in each forest type by multiplying monthly habitat-specific density estimates (D_{ii}) by the spatial extent of each forest type.

Results

Spatio-temporal fluctuations in orangutan density and ecological conditions in the study site

Orangutan density on transects (D_{ij}) varied by more than an order of magnitude across the study period (range 0.63–6.63, mean $(\bar{x}) \pm$ standard deviation (σ) : 2.22 ± 1.05 individuals km⁻², Online Resource 1a), reflecting changes in abundance

as individual orangutans moved in and out of the study site. Peat swamp supported the highest mean density $(\bar{x} \pm \sigma; 4.2 \pm 3.8 \text{ individuals } \text{km}^{-2})$, followed by alluvial bench $(\bar{x} \pm \sigma; 3.2 \pm 3.4 \text{ individuals } \text{km}^{-2})$, lowland sandstone $(\bar{x} \pm \sigma; 3.2 \pm 3.2 \text{ individuals } \text{km}^{-2})$, and freshwater swamp $(\bar{x} \pm \sigma; 2.1 \pm 1.9 \text{ individuals } \text{km}^{-2})$. Average densities were lower at higher elevations: lowland granite $(\bar{x} \pm \sigma; 1.2 \pm 1.3 \text{ individuals } \text{km}^{-2})$, upland granite $(\bar{x} \pm \sigma; 1.1 \pm 1.3 \text{ individuals } \text{km}^{-2})$, and montane forests $(\bar{x} \pm \sigma; 0.5 \pm 0.5 \text{ individuals } \text{km}^{-2})$. Because individual orangutans move among forest types, mean abundance measures are best interpreted as measures of habitat use (i.e., area occupation densities sensu Altmann 1974), rather than indicators of habitat-specific carrying capacity.

There was also considerable temporal variation in ecological variables across the study site: the total stems with mature or ripe fruit varied from 1.3 to 75.4 stems per hectare per month ($\bar{x} \pm \sigma$: 24.3 ± 10.5, Online Resource 1b), rainfall varied from 7.6–176.9 mm/month ($\bar{x} \pm \sigma$: 66.8 ± 32.3, Online Resource 1c), maximum monthly temperature fluctuated between 25.5 and 29.9 °C ($\bar{x} \pm \sigma$: 27.8 ± 0.8) and minimum monthly temperature varied from 18.7 to 22.1 °C ($\bar{x} \pm \sigma$: 20.7 ± 0.6, Online Resource 1d).

Patterns of temporal variation within forest types

Orangutan densities within each forest type varied substantially over time. Monthly density estimates in each forest type varied by at least an order of magnitude, with the greatest range of variation in the alluvial bench (0.8–21.6 individuals km⁻²) and the smallest range in the montane forest (0.1–4.7 individuals km⁻²; Online Resource 2). Orangutan densities were the most stable in the peat swamp (coefficient of variation (CV)=0.91) and freshwater swamp (CV=0.93); they were least stable in the upland granite (CV=1.20) and montane forests (CV=1.29).

Spatiotemporal dispersion among forest types

The highest proportion of individuals were found in peat swamp forests (mean monthly proportion of orangutans at the site = 0.26) and the lowest in montane forests (mean proportion = 0.04). Despite these substantial differences, every forest type was heavily utilized at some point during the study (Fig. 3h). For example, in October of 2012 the lowland sandstone forest contained over 75% of all orangutans encountered in the study site (Fig. 3d). And although montane forests generally contained a small proportion of the total number of individuals, in mid 2011 over 50% of all orangutans in the study site were found there (Fig. 3a). Every forest type held over 40% of individuals in at least one month. In addition, each forest type had at least one period of several consecutive months when orangutans were virtually never encountered (e.g., there were three times when the peat swamp contained less than 5% of individuals for at least four consecutive months, Fig. 3g).

Fig. 2 Spatial variation in orangutan density. Violin plots of estimated monthly orangutan density in each forest type. Violin plots show full range of variation (i.e., all outliers are present) and are overlaid with boxplots where the median value is indicated by a horizontal orange bar. White circles show mean values. Elevation increases from left to right



Fig. 3 Spatiotemporal orangutan density by forest type. The panels depict temporal variation in the proportion of the total orangutan sightings in the study area found in each forest type. The bottom panel shows all seven forest types together, highlighting the substantial temporal fluctuations in dispersion among forest types



Covariation in orangutan density and fruit availability among forest types

Orangutan densities were not highly correlated over time among forest types. Among the five floristically-similar "lowland" habitats (freshwater swamp, alluvial bench, lowland sandstone, lowland granite, and upland granite; Cannon and Leighton 2004), monthly density estimates were generally positively correlated (mean correlation (r) = 0.14, range - 0.02 to 0.28; Online Resource 3). The densities in these forest types were generally negatively correlated with the densities in the peat swamp (mean r = - 0.05) or montane forest (mean r = -0.03). Covariation in phenological measurements shows that the five "lowland" habitats exhibited relatively high synchrony in fruit production (mean r = 0.68, range 0.37–0.86) while the peat swamp and montane forest were less strongly correlated with the lowland forest types (r = 0.36 and 0.41, respectively; Online Resource 5).

Orangutan density was positively correlated with fruit abundance in each of the lowland forest types (mean $r(\bar{r})=0.27$, range = 0.17–0.40), but negatively correlated in the peat swamp (r=-0.03) and montane forest (r=-0.13, see diagonal in Table 1 and Online Resource 2). Orangutan density in the peat swamp and montane forest was

Table 1 Pairwise correlations in orangutan density (individuals km^{-2} , column heads) and plant productivity (number of stems with mature or ripe fruit, row heads) by forest type

	PS orangutans	FS orangutans	AB orangu- tans	LS orangu- tans	LG orangu- tans	UG orangu- tans	MO orangu- tans	Overall mean
PS fruit	- 0.03	0.16	- 0.06	0.03	- 0.08	0.00	- 0.06	- 0.01
FS fruit	- 0.15	0.17	0.30	0.24	0.26	0.09	0.00	0.13
AB fruit	-0.17	0.19	0.40	0.36	0.19	0.23	- 0.14	0.15
LS fruit	-0.14	0.16	0.33	0.33	0.26	0.15	-0.08	0.14
LG fruit	- 0.11	0.14	0.33	0.35	0.24	0.13	- 0.13	0.14
UG fruit	- 0.09	0.16	0.32	0.13	0.16	0.21	- 0.25	0.09
MO fruit	- 0.21	0.15	0.08	0.25	0.13	0.07	-0.13	0.05
Mean cor- relation with FS-UG	- 0.13	0.16	0.34	0.28	0.22	0.16	- 0.12	0.13

Forest types are indicated by two letter codes: peat swamp (PS), freshwater swamp (FS), alluvial bench (AB), lowland sandstone (LS), lowland granite (LG), upland granite (UG), and montane (MO). Correlations between orangutan density and fruit availability with the same forest type are italicized; the bottom row shows the mean correlations of orangutan density with fruit availability in the five lowland habitats (i.e., FS, AB, LS, LG, UG). "Overall mean" column shows row means

negatively correlated with fruit availability in all other forest types (peat: $\bar{r} = -0.13$, range -0.09 to -0.21; montane: $\bar{r} = -0.12$, range = 0.0 to -0.25, Table 1).

Modeling spatiotemporal movements

Higher values for expected orangutan abundance, λ_{ti} , were generally associated with larger values for fruit abundance, and at higher elevations with lower rainfall and higher minimum temperatures (Fig. 4). Specifically, expected abundance increased most rapidly with forest-specific fruit availability in the lowland sandstone and alluvial bench forests, whereas fruit had more moderate effects in the other "lowland" forest types and was a weak predictor of abundance in the peat swamp and montane forests (Fig. 4a, b). Rainfall was generally an unreliable predictor of orangutan abundance, with the exception of montane forests in which orangutan abundance was strongly negatively affected by rainfall (Fig. 4c, d); each increase of 1 mm in rainfall per month decreased expected orangutan abundance in montane forest by 52%. Maximum temperature was a generally unreliable predictor (Fig. 4e, f), while minimum temperature had a positive effect on modeled abundance in the upland granite and montane forest types (Fig. 4g, h). Specifically, each 1 °C increase in minimum temperature increased expected orangutan abundance by 37% in the upland granite and 77% in the montane forest.

Discussion

Our long time series of systematically sampled orangutan sightings coupled with fine-grained data on habitat productivity and abiotic conditions across a diverse landscape at the Cabang Panti Research Station provides much greater resolution than has previously been possible and reveals a remarkable degree of spatial and temporal dynamism in orangutan dispersion along an elevational and productivity gradient. Here we consider our initial hypotheses in the light of these results and highlight important, related insights emerging from our analysis. We then discuss potential sources of error or bias and end with a brief consideration of the applicability of our results for other large-bodied vertebrates.

Landscape-level movements buffer orangutans against fruit scarcity

Our average density estimates are comparable to previously published values from our site (Johnson et al. 2005; Marshall et al. 2014) and towards the high end of orangutan densities in comparable forest types elsewhere in Borneo (Husson et al. 2009). Substantial temporal variation in dispersion among the forest types (Fig. 3h) and large fluctuations in the total number of animals within the study site (Online Resource 1a), however, reveal that individual orangutans frequently moved across the landscape. Our model shows that expected orangutan abundances were generally associated with larger values of fruit abundance (Fig. 4a), suggesting that orangutans switch among the forest types to buffer themselves against fruit scarcity, as expected (H1). These switches are likely driven by their strong preference for large fruit crops from rare, preferred plant taxa (Leighton and Leighton 1983; Leighton 1993). This conclusion is consistent with direct and indirect observations from other sites (e.g., Buij et al. 2002; Djodjosudharmo and van Schaik



1992; Kanamori et al. 2017; Leighton and Leighton 1983, Singleton and van Schaik 2001, te Boekhorst et al. 1990).

Our results provide clear evidence of the mechanisms sunderlying the observation that sites with habitat mosaics t

support higher long-term densities of orangutans than more homogenous ones (Husson et al. 2009). At heterogeneous sites, asynchronies in fruiting phenology among forest types—and especially between the peat swamp, lowlands, **<**Fig. 4 Covariate effects by forest type. The left column indicates back transformed β coefficients (i.e., odds ratios) for the forest type-specific effects of fruit availability **a**, rainfall **c**, maximum temperature **e**, and minimum temperature **g** on orangutan population density. Each plot holds all other predictors at their mean values for each respective forest type (e.g., panel **a** plots the multiplicative effects of an additional stem of mature or ripe fruit per ha holding rainfall, maximum temperature, and minimum temperature at their mean values). Thin and thick lines indicate 95% and 50% confidence intervals, respectively. The right column plots expected orangutan abundance in each forest type as a function of fruit availability **b**, rainfall **d**, maximum temperature **f**, and minimum temperature **h**. Forest type abbreviations on right hand side are the same as in Table 1

and montane forests (Online Resource 4)–provide orangutans with more opportunities to feed on mature and ripe fruits than at sites where they only have access to a single forest type. Orangutan females have substantially smaller home ranges than males (Singleton and van Schaik 2001), which may mean they are more restricted in their ability to switch among forest types. However, although female home ranges at our site are estimated to be 595 ha (Knott et al. 2008), they are generally spatially organized in such a way that they contain at least four forest types (see Fig. 3 in Knott et al. 2008). The habitat mosaic means individuals can often escape the most extreme periods of fruit scarcity while benefitting from peaks in fruit production in multiple habitats.

We note, however, that habitat heterogeneity is one of several factors likely to be responsible for inter-site variation in orangutan density. For example, Vogel et al. (2015) report almost twofold variation in density between the peat swamp sites Tuanan and Sabangau in Central Kalimantan. They attribute the substantially higher density at Tuanan (which, at 4.3–4.5 individuals km⁻², is comparable to the density in peat swamp at CPRS) to the higher nutritional quality of food plants at Tuanan that likely results from nutrient inputs during occasional alluvial floods (Vogel et al. 2015). Other factors are likely important in determining orangutan density as well, such as floristic composition, disturbance, and hunting pressure (Husson et al. 2009; Marshall et al. 2009).

Peat swamp forests are crucially important fallback habitats

Our analysis reveals that the five "lowland" forest types are preferred habitats—orangutan use of these habitats is positively correlated with habitat-specific fruit abundance (Online Resource 2c,e,g,i,k) and expected abundance increases when more fruit is available, holding other predictors at their mean values (Fig. 4b). In contrast, peat swamp and montane forests are fallback habitats that orangutans move to during periods when fruit in the lowland forest types is scarce (Cannon et al. 2007a, b; Marshall 2018; *cf* fallback foods whose consumption is inversely related to the abundance of preferred foods, Marshall and Wrangham 2007). Thus, use of the peat swamp and montane forests is negatively correlated with fruit abundance in the other forest types (Table 1) rather being positively related to fruit abundance in the fallback habitats themselves (Online Resource 2a, m). In short, orangutans are pushed into fallback habitats due to fruit scarcity in preferred habitats, rather than being pulled into them by the resources available in the montane and peat swamp forests themselves.

Of the two fallback habitats, the peat swamp is far more important than montane forest because it sustains higher long-term orangutan densities (i.e., area occupation density is higher; Fig. 2). This is likely because peat swamps lack the super-annual mast fruiting and subsequent periods of extreme fruit scarcity characteristic of the lowland forest types (Cannon et al. 2007b; Marshall et al. 2009), thus providing a more stable food supply (Online Resource 2n). Peat swamps also have relatively high densities of figs (Marshall et al. 2014), which serve as important fallback foods for many vertebrates (Sugardjito et al. 1987; Kinnaird and O'Brien 2005; Dillis et al. 2015; Corlett 2017). The ecological attributes that make peat swamps fallback habitats for orangutans may make them similarly valuable to other taxa with the ability to move widely among forest types in this ecosystem (e.g., sun bears Helarctos malayanus, bearded pigs Sus barbatus, some hornbills Family Bucerotidae; Marshall et al. 2014). The importance of peat swamps for carbon sequestration is well known (Page et al. 2002; Paoli et al. 2010); our results suggest they play a role as an important keystone habitat for vertebrate frugivores as well.

Temperature and rainfall matter, but only at high elevations

Our second hypothesis-that movement patterns and habitat use are sensitive to abiotic conditions-received mixed support. Rainfall and minimum temperature had strong effects on expected abundance in high elevation forests. Specifically, in montane forests orangutan density decreased substantially with increased rainfall (Fig. 4c, d) and increased dramatically at higher minimum temperatures (Fig. 4g, h). Effects were qualitatively similar, although more muted, in the upland granite forest. In lower elevation forests, these effects disappeared or, in some cases, reversed. These patterns are likely due to thermoregulatory constraints, which led orangutans to avoid high elevations at times when conditions were cold (<18 $^{\circ}$ C) and wet and occupy them at densities comparable to the highest quality lowland habitats when conditions were warm (>23 °C) and dry. Orangutans' combination of solitary living and habitual use of night nests likely make inhabiting the montane forests when they are cold and wet both uncomfortable and metabolically costly, especially when coupled with the windy conditions often present on mountain tops.

Our demonstration of the effects of temperature and rainfall can inform habitat suitability projections for orangutans under different climate change scenarios. Examination of long-term weather station and remote sensing data on Borneo suggest the climate is changing to warmer (MoE 2007) and drier conditions (Yatagai et al. 2012), largely as a result of deforestation (Kumagai et al. 2013; McAlpine et al. 2018). These results suggest that montane forests could be used more often by orangutans in the future, a possibility consistent with conclusions from climate models which suggest that upland forests will become more hospitable to lowland mammal species as the global climate changes (Struebig et al. 2015b). Although this possibility offers some hope for long-term orangutan conservation in the face of anticipated changes to climate and land use, we suggest caution in extrapolating our results into the future for several reasons. First, it is possible that changes in climate will affect fruit phenology, crop size, or quality (e.g., Chapman et al. 2018) in ways that may counteract, or intensify, the patterns we report here. Second, our network of 14 weather stations across the landscape in Gunung Palung National Park indicates a more complex picture of trends in rainfall and temperature along the elevational gradient and between the two ridges in our trail system (unpublished data), suggesting that montane forests will not universally become drier and hotter. Third, the value of montane forests as fallback habitats depends on their connection to intact, higher quality lowland forest habitats (Djodjosudharmo and van Schaik 1992; Buij et al. 2002), at least until there has been sufficient time for lowland orangutan food plants to colonize montane forests, a process that will likely lag well behind changes in the climate itself (Marshall and Wich 2016). If the contiguous lowland forests were lost (e.g., to logging, fire, or conversion to oil palm plantations), the montane forests alone likely would not be adequate to support orangutans [i.e., they may be demographic sinks, as they are for ecologicallysimilar gibbons (Marshall 2009) and are likely to be for other vertebrates (Marshall 2018)].

Potential sources of error or bias

We consider the large fluctuations in orangutan encounter rates and dispersion among forest types to be a true reflection of underlying ecological processes, rather than the effects of sampling error or bias for two reasons. First, population densities of species with relatively small, fixed home ranges (gibbons, leaf monkeys) or that live at comparable densities to orangutans (bearded pigs, Prevost's squirrels) at the study site do not fluctuate nearly as much as orangutan densities (Marshall et al., 2014), suggesting that the observed variation in orangutan encounter rates is not due to sampling error or low encounter rates. Second, encounter rates of frugivorous species with small home ranges and stable population densities do not fluctuate as a function of fruit availability (Marshall et al., 2014), suggesting that the positive effects of fruit availability on orangutan abundance are not the result of orangutans being easier to detect during periods of fruit abundance (e.g., because they drop fruits when they are feeding on them).

Land use changes outside the park are similarly unlikely to be responsible for the results we report. Small-scale and industrial agriculture, mining, and logging are changing the landscape surrounding Gunung Palung. These changes are generally directional (e.g., more land is converted from natural forest to oil palm plantations each year), however, rather than fluctuating over time (Fawzi et al. 2018; Zamzani et al. 2009). Thus, it is hard to imagine they are driving the spatial and temporal fluctuations we report here.

Applicability of results for other large-bodied vertebrates

Our results regarding the ecological value of habitat heterogeneity are likely relevant for other large-bodied vertebrates which utilize habitats that are heterogeneous at the scale of individual movements. In the South East Asian tropics, species such as bearded pigs, long-tailed parakeets Psittacula longicauda, helmeted hornbills Buceros vigil, or sun bears that can range widely to track spatio-temporal variation in habitat productivity are likely able to move across the landscape to buffer themselves against resource scarcity (Curran and Leighton 2000; Leighton and Leighton 1983; Marshall et al. 2014). Observations of severely emaciated bearded pigs and sun bears during a period of fruit scarcity at a site without access to multiple forest types (Wong et al. 2000) highlight the potential benefits of habitat heterogeneity for large-bodied frugivores. We also note that while orangutan movements are undoubtedly influenced by factors other than merely resource availability (e.g., competition, sexual coercion), predation-a factor that likely influences movements in many other taxa-is not a major ecological pressure on orangutans on Borneo. Therefore, for species for which predation risk is likely important, models of dispersion dynamics would need to incorporate ecologically-relevant measures of predation risk (e.g., spatio-temporal fluctuations in predator abundance) to adequately characterize dispersion dynamics. Modeling frameworks, such as that which we present here, could readily incorporate predator density (or correlates thereof) as a covariate for these taxa.

More broadly, our results highlight the complexities of studying how long-lived mammals with slow life histories respond to dynamic resource landscapes that exhibit large, unpredictable temporal variation in environmental conditions. Because variation in biotic and abiotic conditions may not be predictably seasonal and can vary dramatically over time (Online Resource 1b,c,d), long-term data at fine spatial scales are necessary to understand spatiotemporal fluctuations in animal dispersion across heterogeneous landscapes. Such efforts are time consuming, but provide valuable insights for ecological theory and applied conservation. Our results show that large-bodied, long-lived species can periodically be abundant in low-quality habitats that likely could not support them in the long-term, and also be virtually absent for extended periods from habitats that are vitally important for sustaining the population. This suggests that we should interpret the results from short-term studies with caution, especially if they are used to inform conservation or management plans.

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Author contribution statement AJM, ML, LB, KLF, and HUW designed the study. AJM and HUW raised funds for data collection; AJM, LGB, ES, TWS, and TMS collected the data and/or provided logistical support; LB, KLF, LGB, MTF, and AJM extracted data and contributed R code; MTF and EFZ developed the Bayesian hierarchical distance sampling model; AJM and HUW wrote the manuscript; AJM produced the figures. All authors contributed to the drafts and gave final approval for publication.

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Data availability All data necessary to reproduce our results are available at figshare.com: DOI m10.6084/m9.figshare.14731866.

Code availability All code necessary to reproduce our results are available at figshare.com https://doi.org/10.6084/m9.figshare.14731890

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

References

- Altmann SA (1974) Baboons, space, time, and energy. Am Zool 14:221–248
- Avgar T, Mosser A, Brown GS, Fryxell JM (2013) Environmental and individual drivers of animal movement patterns across a wide geographical gradient. J Anim Ecol 82:96–106
- Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. Ecol Model 157:281–300
- Boyce MS, Johnson CJ, Merrill EH et al (2016) Can habitat selection predict abundance? J Anim Ecol 85:11–20
- Boyko RH, Marshall AJ (2010) Using simulation models to evaluate ape nest survey techniques. PLoS ONE 5:754
- Brockman DK, van Schaik CP (eds) (2005) Seasonality in primates: studies of living and extinct human and non-human primates. Cambridge University Press, Cambridge
- Buckland ST, Anderson D, Burnham K et al (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, U.K.
- Buij R, Wich SA, Lubis AH, Sterck EHM (2002) Seasonal movements in the Sumatran orangutan (*Pongo pygmaeus abelii*) and consequences for conservation. Biol Cons 107:83–87
- Cannon CH, Leighton M (2004) Tree species distributions across five habitats in a Bornean rain forest. J Veg Sci 15:257–266
- Cannon CH, Curran LM, Marshall AJ, Leighton M (2007a) Longterm reproductive behaviour of woody plants across seven Bornean forest types in the Gunung Palung National Park (Indonesia): suprannual synchrony, temporal productivity and fruiting diversity. Ecol Lett 10:956–969
- Cannon CH, Curran LM, Marshall AJ, Leighton M (2007b) Beyond mast-fruiting events: Community asynchrony and individual dormancy dominate woody plant reproductive behavior across seven Bornean forest types. Curr Sci 00113891(93):1558–1566
- Chapman CA, Valenta K, Bonnell TR et al (2018) Solar radiation and ENSO predict fruiting phenology patterns in a 15-year record from Kibale National Park, Uganda. Biotropica 50:384–395
- Charnov EL, Orians GH, Hyatt K (1976) Ecological implications of resource depression. Am Nat 110:247–259
- Clucas B, McHugh K, Caro T (2008) Flagship species on covers of US conservation and nature magazines. Biodiv Cons 17:1517–1528
- Corlett RT (2017) Frugivory and seed dispersal by vertebrates in tropical and subtropical Asia: an update. Glob Ecol Conserv 11:1–22
- Curran LM, Leighton M (2000) Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. Ecol Mono 70:101–128
- Dillis C, Beaudrot L, Clink DJ et al (2015) Modeling the ecological and phenological predictors of fruit consumption by gibbons (*Hylobates albibarbis*). Biotropica 47:85–93
- Djojosudharmo S, van Schaik CP (1992) Why are orangutans so rare in the highlands? Altitudinal changes in a Sumatran forest. Trop Biodivers 1:11–22
- Fawzi NI, Husna VN, Helms JA (2018) Measuring deforestation using remote sensing and its implication for conservation in Gunung Palung National Park, West Kalimantan, Indonesia. IOP Conf Ser Earth Environ 149:38
- Gregory SD, Brook BW, Goossens B et al (2012) Long-term field data and climate-habitat models show that Orangutan persistence depends on effective forest management and greenhouse gas mitigation. PLoS ONE 7:e43846
- Husson SJ, Wich SA, Marshall AJ et al (2009) Orangutan distribution, density, abundance and impacts of disturbance. In: Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP (eds) Orangutans: geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford, pp 77–96

- Johnson AE, Knott CD, Pamungkas B et al (2005) A survey of the orangutan (*Pongo pygmaeus wurmbii*) population in and around Gunung Palung National Park, West Kalimantan, Indonesia based on nest counts. Biol Cons 121:495–507
- Kanamori T, Kuze N, Bernard H et al (2017) Fluctuations of population density in Bornean orangutans (*Pongo pygmaeus morio*) related to fruit availability in the Danum Valley, Sabah, Malaysia: a 10-year record including two mast fruitings and three other peak fruitings. Primates 58:225–235
- Karr JR, Freemark KE (1983) Habitat selection and environmental gradients: dynamics in the "stable" tropics. Ecology 64:1481–1494
- Kellner K (2016) jagsUI: A Wrapper Around "rjags" to Streamline "JAGS" Analyses. https://CRAN.R-project.org/package=jagsUI. Accessed 3 Aug 2020
- Kelt DA, Heske EJ, Lambin X et al (2019) Advances in population ecology and species interactions in mammals. J Mammal 100:965–1007
- Kéry M, Royle JA (2016) Applied hierarchical modeling in ecology. Academic Publishers, Waltham
- Kinnaird MF, O'Brien TG (2005) Fast foods of the forest: the influence of figs on primates and hornbills across Wallace's line. In: Lawrence Dew J, Boubli JP (eds) Tropical fruits and frugivores: the search for strong interactors. Springer, Dordrecht, pp 155–184
- Knott CD (2001) Female reproductive ecology of the apes: implications for human evolution. In: Ellison PT (ed) Reproductive ecology and human evolution, pp 429–463
- Knott C, Beaudrot L, Snaith T et al (2008) Female-female competition in Bornean orangutans. Int J Primatol 29:975–997
- Kumagai T, Kanamori H, Yasunari T (2013) Deforestation-induced reduction in rainfall. Hydrol Process 27:3811–3814
- Leighton M (1993) Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. Int J Primatol 14:257–313
- Leighton M, Leighton DR (1983) Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: Whitmore STC, Chadwick AC (eds) Tropical rain forest: ecology and management, vol 2. Blackwell Scientific Publications, Palo, pp 181–196
- Manly BF, McDonald L, Thomas D et al (2002) Resource selection by animals: statistical design and analysis for field studies, 2nd edn. Kluwer Academic Publishers, Dordrecht
- Marshall AJ (2009) Are montane forests demographic sinks for Bornean white-bearded gibbons *Hylobates albibarbis*? Biotropica 41:257–267
- Marshall AJ (2018) Conservation science in the tropics: why so much ecological research is useless, and why we need more of it. In: Primatology, bio-cultural diversity and sustainable development in tropical forests. UNESCO, Mexico City, Mexico
- Marshall AJ, Meijaard E (2009) Orang-utan nest surveys: the devil is in the details. Oryx 43:416–418
- Marshall AJ, Wich SA (2016) Some future directions for primate conservation research. In: Wich SA, Marshall AJ (eds) An introduction to primate conservation. Oxford University Press, Oxford, pp 287–296
- Marshall AJ, Wrangham RW (2007) Evolutionary consequences of fallback foods. Inter J Primatol 28:1219–1235
- Marshall AJ, Ancrenaz M, Brearley FQ et al (2009) The effects of forest phenology and floristics on populations of Bornean and Sumatran orangutans. In: Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP (eds) Orangutans: geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford, pp 97–118
- Marshall AJ, Beaudrot L, Wittmer HU (2014) Responses of primates and other frugivorous vertebrates to plant resource variability over

space and time at Gunung Palung National Park. Int J Primatol 35:1178–1201

- Mason TH, Fortin D (2017) Functional responses in animal movement explain spatial heterogeneity in animal-habitat relationships. J Anim Ecol 86:960–971
- Mathewson P, SpeharS ME, Nardiyono P, Sasmirul A, Sudiyanto O, Sulhnudin J, Jumali MAJ (2008) Evaluating orangutan census techniques using nest decay rates: implications for population estimates. Ecol Appl 18:208–221
- McAlpine CA, Johnson A, Salazar A et al (2018) Forest loss and Borneo's climate. Environ Res Lett 13:044009
- McPeek MA, Holt RD (1992) The evolution of dispersal in spatially and temporally varying environments. Am Nat 140:1010–1027
- Meijaard E, Wich SA, Ancrenaz A, Marshall AJ (2012) Not by science alone: why orangutan conservationists must think outside the box. Ann NY Acad Sci 1249:29–44
- Mitra Setia T, Delgado RA, Utami Atmoko SS et al (2009) Social organization and male-female relationships. In: Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP (eds) (2009) Orangutans: geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford, pp 245–253
- MoE (2007) Indonesia country report: climate variability and climate change, and their implication. Indonesian Ministry of Environment, Jakarta
- Oliver T, Roy DB, Hill JK et al (2010) Heterogeneous landscapes promote population stability. Ecol Lett 13:473–484
- Page SE, Siegert F, Rieley JO et al (2002) The amount of carbon released from peat and forest fires in Indonesia during 1997. Nature 420:61–65
- Paoli GD, Wells PL, Meijaard E, Struebig MJ, Marshall AJ, Obidzinski K, Slik JF (2010) Biodiversity in the REDD. Why efforts to reduce anthropogenic carbon emissions from forest may undermine long-term biodiversity conservation in Indonesia. Carbon Balance Manag 5:7
- Plummer M (2003) rjags: Bayesian Graphical Models Using MCMC. Retrieved from http://cran.r-project.org/package=rjags. Accessed 3 Aug 2020
- Presley SJ, Cisneros LM, Klingbeil BT, Willig MR (2019) Landscape ecology of mammals. J Mammal 100:1044–1068
- Pulliam HR (1988) Sources, sinks, and population regulation. Am Nat 132:652–661
- R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rosenzweig ML (1991) Habitat selection and population interactions: the search for mechanism. Am Nat 137:S5–S28
- Shine R, Brown GP (2008) Adapting to the unpredictable: reproductive biology of vertebrates in the Australian wet–dry tropics. Philos Trans R Soc Lond B 363:363–373
- Singleton I, van Schaik CP (2001) Orangutan home range size and its determinants in a Sumatran swamp forest. Int J Primatol 22:877–911
- Spehar SN, Sheil D, Harrison T, Louys J, Ancrenaz M, Marshall AJ, Meijaard E (2018) Orangutans venture out of the rainforest and into the Anthropocene. Sci Adv 4(6):e1701422
- Struebig MJ, Fischer M, Gaveau DL et al (2015a) Anticipated climate and land-cover changes reveal refuge areas for Borneo's orang-utans. Global Change Biol 21:2891–2904
- Struebig MJ, Wilting A, Gaveau DLA et al (2015b) Targeted conservation to safeguard a biodiversity hotspot from climate and land-cover change. Curr Biol 25:372–378
- Sugardjito J, Te Boekhorst IJ, Van Hooff JARAM (1987) Ecological constraints on the grouping of wild orangutans (*Pongo pyg-maeus*) in the Gunung Leuser National Park, Sumatra, Indonesia. Int J Primatol 8:17–41
- te Boekhorst IJ, Schürmann CL, Sugardjito J (1990) Residential status and seasonal movements of wild orang-utans in the

Gunung Leuser Reserve (Sumatera, Indonesia). Anim Behav 39:1098–1109

- Van Moorter B, Bunnefeld N, Panzacchi M et al (2013) Understanding scales of movement: animals ride waves and ripples of environmental change. J Anim Ecol 82:770–780
- van Noordwijk MA, Atmoko SS, Knott CD et al (2018) The slow ape: high infant survival and long interbirth intervals in wild orangutans. J Hum Evol 25:38–49
- Vogel ER, Harrison ME, Zulfa A et al (2015) Nutritional differences between two orangutan habitats: implications for population density. PLoS ONE 10:e0138612
- Wich SA, van Schaik CP (2000) The impact of El Nino on mast fruiting in Sumatra and elsewhere in Malesia. J Trop Ecol 16:563–577
- Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP (eds) (2009) Orangutans: geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford

- Wisdom MJ, Nielson RM, Rowland MM, Proffitt KM (2020) Modeling landscape use for ungulates: forgotten tenets of ecology, management, and inference. Front Ecol Evol 8:1–9
- Wong ST, Servheen C, Ambu L, Norhayati A (2000) Impacts of fruit production cycle on Malayan sun bears and bearded pigs in lowland tropical rainforest of Borneo. J Trop Ecol 21:627–639
- Yatagai A, Kamiguchi K, Arakawa O et al (2012) APHRODITE: constructing a long-term daily gridded precipitation dataset for Asia based on a dense network of rain gauges. Bull Am Meteorol Soc 93:1401–1415
- Zamzani F, Onda N, Yoshino K, Masuda M (2009) Deforestation and agricultural expansion processes in Gunung Palung National Park, West Kalimantan, Indonesia. Jurnal Manajemen Hutan Tropika 15:24–31

Electronic Supplementary Material

Biotic and abiotic drivers of dispersion dynamics in a large-bodied tropical vertebrate, the Western Bornean orangutan

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- ESM 2. Temporal variation within forest types
- ESM 3. Pairwise correlations in orangutan density among forest types
- ESM 4. Pairwise correlations in plant productivity among forest types

ESM 1. Time series of orangutan density and ecological covariates. Orangutan density (a), the number of stems with mature or ripe fruit (b), rainfall (c) and maximum and minimum temperature (d) in the study site from October 2007 to December 2015. Shading indicates 95% confidence intervals. All numbers are averaged across all forest types.



ESM 2. Temporal variation within forest types. The left panels depict the relationship between fruit availability and orangutan density in the seven forest types. Lines and gray shaded regions depict the mean and 95% confidence intervals of predicted orangutan density using a simple linear model. In the "lowland" forest types (panels B-F) fruit availability was a reliable positive predictor of orangutan density; fruit availability was not a reliable predictor of density in the montane forest (A) or the peat swamp (G). The right panels depict temporal variation in orangutan density (D_{tj} , line) and fruit availability (% stems with mature or ripe fruit, gray bars) in the seven sampled forest types.



ESM 3. Pairwise correlations in orangutan density among forest types. Forest types are indicated by two letter codes: peat swamp (PS), freshwater swamp (FS), alluvial bench (AB), lowland sandstone (LS), lowland granite (LG), upland granite (UG), and montane (MO). Correlations among lowland forest types (FS, AB, LS, LG, UG) are shaded; the bottom row shows the mean correlations between the orangutan density in the column header and lowland forest types. "Overall mean" shows row means.

Orangutan density	PS	FS	AB	LS	LG	UG	мо	Overall mean
PS		-0.11	-0.13	-0.06	-0.13	0.16	-0.01	-0.05
FS	-0.11		0.21	0.10	0.06	-0.03	-0.09	0.03
AB	-0.13	0.21		0.28	0.26	0.17	-0.05	0.12
LS	-0.06	0.10	0.28		0.08	0.14	-0.08	0.08
LG	-0.13	0.06	0.26	0.08		0.08	0.02	0.06
UG	0.16	-0.03	0.17	0.14	0.08		0.05	0.10
МО	-0.01	-0.09	-0.05	-0.08	0.02	0.05		-0.03
Mean correlation with FS-UG	-0.05	0.09	0.23	0.15	0.12	0.09	-0.03	0.08

Fruit availability	PS	FS	AB	LS	LG	UG	МО	Overall mean
PS		0.32	0.36	0.36	0.42	0.32	0.25	0.34
FS	0.32		0.60	0.59	0.71	0.37		0.52
AB	0.36	0.60		0.80	0.86	0.64	0.57	0.64
LS	0.36	0.59	0.80		0.83	0.63	0.35	0.59
LG	0.42	0.71	0.86	0.83		0.74	0.45	0.67
UG	0.32	0.37	0.64	0.63	0.74		0.36	0.51
МО	0.25	0.29	0.57	0.35	0.45	0.36		0.38
Mean correlation with FS-UG	0.36	0.57	0.73	0.72	0.78	0.60	0.43	0.60

ESM 4. Pairwise correlations in plant productivity (number of stems with mature or ripe fruit) among forest types. Correlations among lowland forest types are shaded; the bottom row shows the mean correlations among the shaded lowland forest types. "Overall mean" shows row means. Forest type codes are the same as in ESM 4.