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Research Article

Investigating constraints on the survival of orangutans across Borneo and Sumatra

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Abstract
Orangutans are highly endangered. In order to implement effective conservation strategies for these species, it is crucial to understand fully what constrains their distribution. Here, we use a previously developed time budget model to investigate the factors constraining the orangutans' ability to inhabit different areas of Borneo and Sumatra, as well as the social group size they are potentially able to adopt in their habitats. This model uses data from 13 field sites, together with climate and environmental data, to predict the amount of time individuals would need to spend in each of four main activities – feeding, moving, resting, and socializing. We found that resting time, which was linked to both dietary constraints and forest cover, was a key behavioral limitation on orangutan distribution. The maximum possible group size predicted for orangutans was low over the entire range, indicating that ecological constraints limit orangutan sociality, and that even small changes to habitat quality may further reduce the maximum possible group size. The fact that the values are already approaching one in many locations and are low throughout both Borneo and Sumatra, suggests that orangutans are vulnerable to extinction over their entire current distribution.

Key Words: Orangutan, conservation, biogeographical distribution, time budget modelling

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Introduction

The distribution of orangutans (*Pongo sp.*) has been dramatically reduced since the Early Pleistocene, driven by a combination of climate change and the impact of the arrival and expansion of human populations [1-3]. Orangutans are now highly threatened with extinction [4] and survive only in the fragmented rainforests of Borneo and Sumatra. Despite the work of conservation organizations and government departments to reduce deforestation and bring a halt to the pet trade and hunting, these factors continue to deplete remaining populations [5]. As habitats become increasingly fragmented and degraded, it is essential to gain a detailed understanding of the specific habitat needs of the orangutan, so that conservation resources can be focused on the most appropriate areas and issues.

To understand the habitat needs and distribution of a species, it is important to know not only why a species lives in a given environment, but also why it does not live in others [6]. The ultimate determinants of distribution patterns are the climate and the environment. However, to gain a more detailed understanding of the distribution of species, it is useful to look at the proximate restrictions on survival, such as behavior, which interfaces between the climate/environment and the ability of a species to survive [7]. For example, if feeding trees are widely spaced in the environment, in order to find enough food to meet its energetic requirements an animal may have to spend more time moving than is available per day. Understanding which behaviors may prevent survival of a species in a given habitat can reveal exactly how the environment restricts biogeography [8].

In gregarious species, social group size is an additional factor that can limit biogeographical distribution. If the habitat cannot support a group of a viable size, the survival of the species may be jeopardized [8, 9]. Orangutans are primarily solitary animals, although they do form larger, relatively stable groups during periods of high mating activity [10] or during periods of greater food availabilty [11]. It is thought that orangutans' solitary social organization may be due to the high ecological costs of grouping [12]. The costs of larger groups could include feeding competition or additional travel time, needed to find enough food for every individual in the group. The dipterocarp forests in which orangutans are predominantly living are indeed a relatively unproductive environment [13]. Fruit, the main food source for orangutans, is patchily distributed in both space and time [14], in small clumps relative to the size of an orangutan [15]. Low group sizes therefore appear to be a beneficial strategy to reduce the costs of feeding competition [12]. This is supported by evidence that average party size

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is larger at more productive sites [10], and in captivity orangutans show higher frequencies of social behavior than in the wild, including regular grooming [16-19]. If it is indeed ecological constraints that are restricting orangutan sociality, this suggests that they may already be close to the edge of their ability to survive in their current habitat, and together with their extremely slow life history, this makes the species particularly vulnerable to further habitat degradation.

As the rainforests continue to be diminished at a rapid pace [20], and conservation funds remain relatively limited, it will not be possible to protect all remaining orangutan habitats. Choices will have to be made about where resources should be focused [21]. Such choices will be influenced by topography, proximity to towns and roads, vulnerability to logging, and the value of the land for commercial purposes [22]. However, an additional understanding of the ecological suitability of the land for the orangutan is needed, so that areas where the orangutan has the greatest chance of survival can be preserved in preference to those where the orangutan's survival is more precarious. Orangutans have extremely slow reproductive rates, producing offspring only every nine years on average [23]. Even populations experiencing no external threats only grow at a rate of two percent annually, so that even in the best quality habitats, a hunting rate of only two or three percent would quickly lead to extinction [24]. It is therefore absolutely critical to protect habitat where orangutan population sizes are sustainable or have the potential to grow, and ecological suitability is a key parameter that must be assessed.

Determining the factors affecting habitat suitability for orangutans as well as their social behavior will help to focus conservation resources for these species. Time budget modelling is a powerful way to address these issues [8]. Time budget models can be used to investigate how the environment, through its effects on behavior, shapes biogeography and social organization [25]. These models provide valuable insights into the factors that determine the habitats in which a species can live [7, 25-29], the group sizes that they can adopt [9, 30], and the amount of time budgeting stress that they face in any given environment [8, 31]. Time budget models can therefore provide an indication of habitat suitability for conservation planning. Here, we use time budget modelling to investigate the behavioral and social factors that limit orangutan distribution patterns. Both species of orangutan are included in the model and where we refer to orangutans, this encompasses both the Bornean species (*Pongo pygmaeus*) and the Sumatran species (*Pongo abelii*).

Methods

Time budget models

Time budget models use existing relationships between climatic, dietary and demographic variables, and behavior, to predict the amount of time that animals need to devote to each activity under different climatic and thus environmental conditions [8]. The climate affects individual behavior through direct effects on the animals (*e.g.,* thermoregulation) as well as indirect effects on vegetation quality and distribution, which can in turn influence diets and the amount of time required for feeding, moving and resting [32, 33]. In addition, for gregarious species, the size of the social group needs to be factored into the models. Group living provides benefits such as a reduction in predation risk; therefore, maintaining a social group larger than the habitat specific minimum (set by the level of predation risk) may be an essential part of a species' survival strategy [34]. Grouping, however, incurs an added demand on an individual's time, for social interaction to maintain group cohesion [9]. Group size can also affect other time budget components, for example through competition for food, leading to an increase in feeding, moving or resting time [35]. Time budget models take these effects into account and allow us to predict not only the presence or absence of a species in a habitat, but also to calculate the expected time budget components as well as possible group sizes for a given location [8]. The group size at which time budget demands fill all available time is the maximum ecologically tolerable group size that can be adopted in a specific location [25]. If this maximum exceeds the habitat (and species-) specific minimum, then the species is predicted to survive in the given location.

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The orangutan time budget model

In this section we briefly summarize the previously developed orangutan time budget model; further details can be found in Carne et al. [43]. Time budget, dietary and demographic data were collated from the literature from 13 study sites in Borneo and Sumatra (Table 1).

Table 1: Group size, time spent feeding, moving and resting, and percentage of time spent eating fruit and leaves at 13 orangutan field sites.

Site	Species/subspecies	Group Size	% Feeding	% Moving	% Resting	% Fruit	% Leaves
Danum[1]	*P. pygmaeus morio*	-	47.2	16.9	34.4	60.9	22.2
Kinabatangan[2]	*P. pygmaeus morio*	-	34.1	10.3	53.6	68.0	22.9
Mentoko[3]	*P. pygmaeus morio*	1.28	45.2	10.4	43.1	53.8	29.0
Ulu Segama[4]	*P. pygmaeus morio*	1.93	32.3	16.4	51.4	51.5	-
Sabangau[5]	*P. pygmaeus wurmbii*	-	61.3	15.9	19.7	73.8	5.1
Cabang Panti[6]	*P. pygmaeus wurmbii*	1.04	36.1	9.9	52.8	70.0	13.4
Tanjung Puting[7]	*P. pygmaeus wurmbii*	1.18	60.1	18.7	18.2	60.9	14.7
Tuanan[8]	*P. pygmaeus wurmbii*	1.13	50.6	16.8	30.9	69.8	17.2
Sungai Lading[9]	*P. pygmaeus wurmbii*	1.03	-	-	-	61.0	-
Batang Seragan[10]	*P. abelii*	-	24.0	15.0	54.0	46.0	13.0
Ketambe[11]	*P. abelii*	2.04	48.2	12.8	38.8	62.8	20.8
Ranun[12]	*P. abelii*	1.85	44.1	16.0	40.0	84.7	10.2
Suaq Balimbing[13]	*P. abelii*	1.90	53.1	17.3	27.2	66.2	15.5

[1][56]; [2][57]; [3][58-61]; [4][62]; [5][57]; [6][10, 41, 57]; [7][63, 64]; [8][42, 57]; [9][42]; [10][50, 65], [11][10, 12, 66]; [12] [62]; [13][10, 67]

Regression equations explaining the percentage of time spent feeding, moving, and resting were created from these observational data, 19 climate variables [36] and the percentage of forest cover [37]. The resulting equations can be found in Table 2. It is important to note that ideally the resting time equation should predict enforced resting time (*i.e.,* the resting time that is required for the digestion of food or for thermoregulation), not uncommitted resting time (a reserve of free time that can be allocated to other essential activities). Enforced resting time is the time an animal needs to devote to resting in order to survive, thus time that cannot be traded off for other activities [31]. However, observed resting time usually consists of both uncommitted time and enforced resting time, and it is difficult to separate these two components. Although a generic equation to predict enforced resting time has been suggested for primates [31], we found that this equation predicted unrealistically low values for orangutans. We therefore generated a species-specific resting time equation for the orangutan model. This resting time equation has a high explanatory power (r^2=0.88) and the relationship with group size is positive (not negative, as would be expected for the effects of food competition and uncommitted time), suggesting that very little resting time in orangutans is in fact uncommitted [7]; thus, we assume that the equation predicts values very close to that required for enforced resting time. However, it is important to note that the values predicted for resting time may be slightly overestimated by the model, as any uncommitted time cannot be separated from overall resting time. Maximum ecologically tolerable group sizes may therefore also be slightly higher than predicted by the model.

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Table 2: Multiple regression equations for time budget and diet variables (see [43]) for details on model equations and their derivation). ^ Temperature seasonality = standard deviation of mean monthly temperatures [°C]*100; † Generic equation from Lehmann et al. [30]

Variable	Equation	R^2_{adj}	N	F	P
% Feeding time	22.081 + 0.665*%forest cover – 0.806*% leaves in diet – 0.032*precipitation [mm] of wettest month	0.91	11	35.99	<0.001
% Moving time	-97.085 + 0.358*temperature seasonality^ – 0.0005*temperature seasonality ^{2} + 0.189*mean temperature [°C] of wettest quarter	0.56	12	5.61	<0.01
% Resting time	128.548 + 27.417*group size – 0.968*% forest cover – 0.176* temperature seasonality	0.88	8	17.58	<0.05
% Fruit in diet	174.100 – 0.488*precipitation [mm] of warmest quarter + 0.0004* precipitation [mm] of warmest quarter ^{2} + 0.267*% forest cover	0.56	13	6.06	<0.05
% Leaves in diet	100 - %fruit in diet				
% Social time	1.01 + 0.23*group size	Generic equation†			

These equations were implemented in ArcGIS version 9.3 [38], using the climate [36] and forest cover data [37], to predict the amount of time required for each of the four key behaviors in every pixel in a raster image of Borneo and Sumatra. The sum of the time budget allocations for each pixel was calculated, and group size was increased until the total time budget allocations exceeded 100%. The maximum ecologically tolerable group size was then defined as the group size of the previous iteration. Human population density (HPD) [39] and land cover [40] data were also incorporated into the model to exclude regions where recent anthropogenic activities prevent orangutan habitation. As orangutans spend the majority of their time alone and have been observed to live in average group sizes as low as 1.03 and 1.04 [41, 42], they were assumed to be able to survive in a location if the predicted maximum group size was greater than or equal to a set minimum of one, and there was a suitable land cover category and an HPD value less than 20 people per square kilometer [43].

Constraints on orangutan biogeography

To identify the behavioral constraints limiting the orangutan's distribution, time budget allocations were compared between the sites that were correctly predicted as suitable for the orangutan ("correct presences") and the sites that were correctly predicted as unsuitable ("correct absences"). In order to perform this analysis, a grid of 374 points separated by 0.5° longitude and latitude was created across Borneo and Sumatra. This improves the independence of the data compared to pixel level resolution. Values for each of the time budget variables were compared within correct presence and correct absence locations that fell on this grid of points. In addition, values were compared between correct presences and false presences (*i.e.,* the areas which were predicted to be suitable habitat, but where the orangutan is not currently found). Again, only points falling on the grid were compared, to ensure the independence of the data. This comparison sheds light on the factors preventing orangutans from living in these apparently suitable habitats. To assess habitat 'quality', we plotted the predicted maximum ecologically tolerable group sizes for the orangutan at all locations throughout Borneo and Sumatra. Areas characterized by low maximum ecologically tolerable group sizes are those in which the orangutan is likely to be under ecological stress because of limited uncommitted time.

Statistical analyses

To assess what restricts orangutan biogeography, we used the Mann-Whitney-U test to compare predicted values for feeding, moving and resting time, and the percentage of fruit in the diet between

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sites where orangutan were correctly predicted to be present and absent, as well as between sites where orangutans were correctly predicted to be present and those where they were incorrectly predicted to be present. The Mann-Whitney-U test was chosen because the data were not normally distributed. To validate the time budget model, we also compared observed group sizes with predicted maximum ecologically tolerable group sizes at each site, using the Wilcoxon Signed Rank Test. All analyses were carried out using SPSS version 17 [44].

Results

Model Predictions

The distribution map for the orangutan based on the time budget model is displayed in Figure 1. The model provided a good fit to the observed data [45, 46], accurately predicting the presence or absence of orangutans in 77% of map pixels [43].

Behavioral Constraints

Comparing the time budget variables among correct absences and presences, we found that resting time was significantly lower (Mann Whitney U test: resting - $z = -5.770$, $N = 288$, $P < 0.001$), while feeding time and the percentage of fruit in the diet were significantly higher (MWU: feeding - $z = -3.830$, $N = 288$, $P < 0.001$; fruit - $z = -2.357$, $N = 288$, $P < 0.05$) in correct presences compared to correct absences (Fig. 2). Moving time did not differ significantly between correct presences and correct absences (MWU test: $z = -0.594$, $N = 288$, $P = 0.552$). This suggests that it is primarily resting time that restricts orangutan distributions.

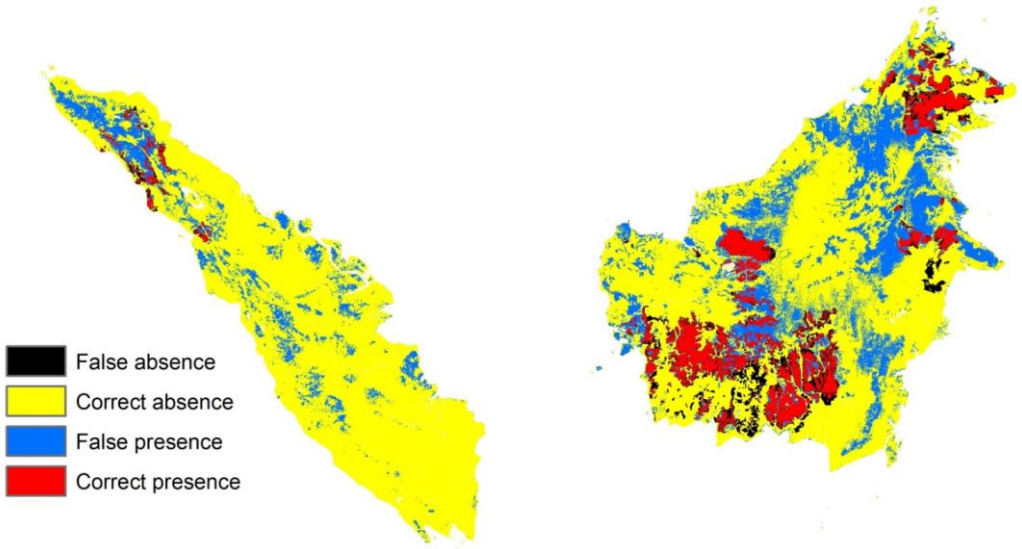


Fig. 1. Predicted distribution of the orangutan from the time budget model compared to the observed distribution. False absences indicate locations where orangutans are present but the model predicted absence; correct absences are locations where orangutans are absent and the model predicted absence; false presences are locations where orangutans are absent and the model predicted presence; and correct presences are locations where orangutans are present and the model predicted presence. From [43].

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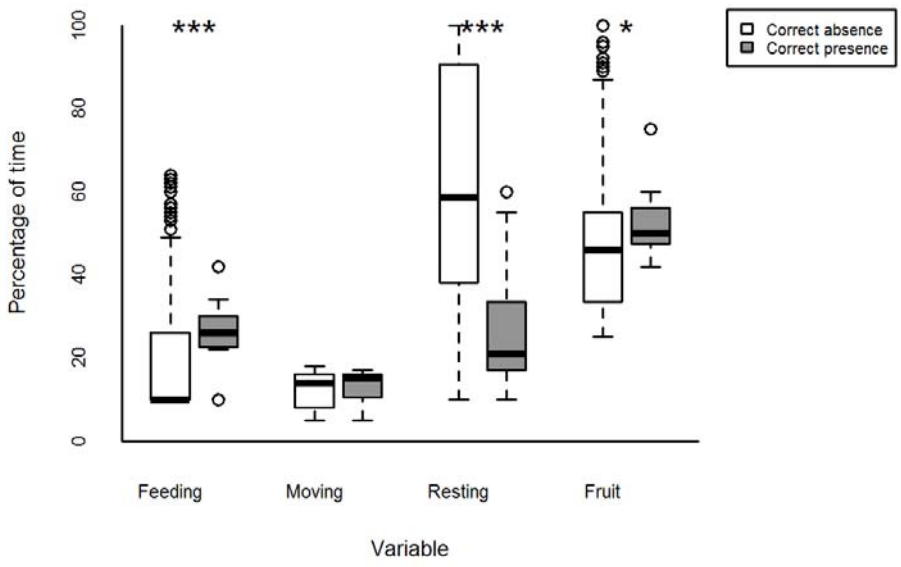


Fig. 2. The predicted percentage of time spent feeding, moving and resting and the percentage of fruit in the diet at sites where orangutans were correctly predicted to be absent and correctly predicted to be present (for all boxplots whiskers represent highest and lowest values and the box represents the upper quartile, median and lower quartile. Dots are outliers, * indicates that P < 0.05 and * indicates that P < 0.001)**

The comparison between sites where orangutans were correctly predicted to be present and those where the model predicted orangutans to live but where they have not been observed, supports the previous conclusions: resting time was significantly higher in locations where orangutans were falsely predicted to be present than those where they were correctly predicted to be present (MWU: z = -3.779, N = 95, P < 0.001; Fig. 3). However, moving time was found to be significantly lower in false presences than correct presences (MWU: z = -3.881, N = 95, P < 0.001), whereas feeding time and the percentage of fruit in the diet did not differ significantly between sites (MWU: feeding - z = -0.356, N = 95, P = 0.722; fruit - z = -1.459, N = 95, P = 0.145). This suggests that resting time, but not feeding time, poses a serious constraint on orangutan distributions.

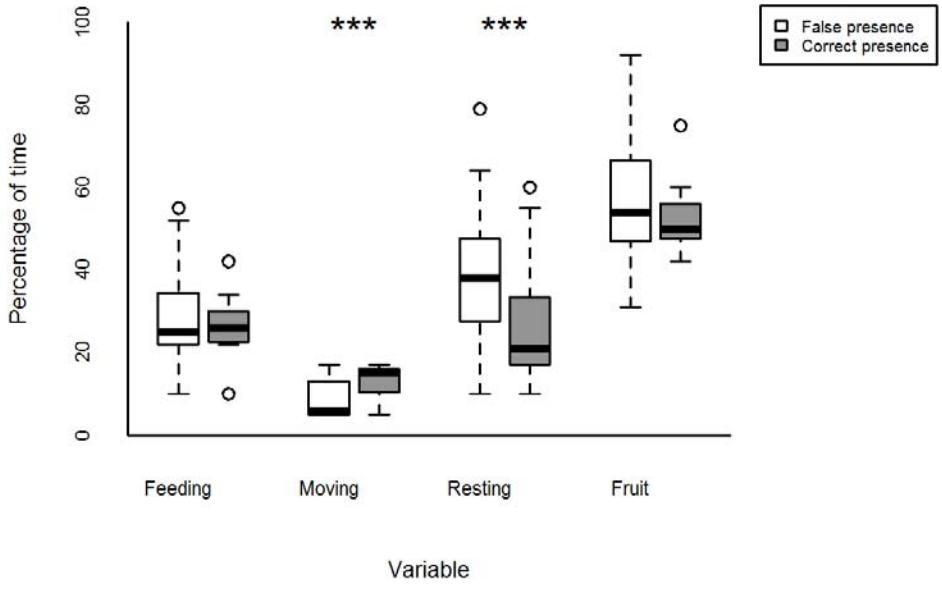


Fig. 3. Percentage time spent feeding, moving and resting and the percentage of fruit in the diet at sites where orangutans were falsely predicted to be present and correctly predicted to be present (* indicates that P < 0.001).**

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Social constraints

Because maximum ecologically tolerable group sizes (METGS) represent the absolute upper limit of group size, observed group sizes should all fall below – and can lie anywhere below - the values predicted for METGS by the model. Predicted values for METGS were indeed all significantly higher than observed group sizes (Wilcoxon Signed Rank Test: z = -2.668, N = 9, P < 0.01; Fig. 4). Group size was not found to affect feeding time, but it was a major predictor of resting time allocations, with resting time demands increasing as group size increased (Table 2), suggesting that feeding competition may lead to an increased reliance on fallback foods requiring longer digestion times. METGS predicted by our time budget model for the islands of Borneo and Sumatra are shown in Figures 5 and 6. Average METGS was slightly higher in Sumatra (mean = 2.25 ± SD 0.50) than in Borneo (mean = 2.16 ± SD 0.38). The maximum predicted group consisted of 3.4 individuals, but this was only predicted for very small areas of northern Borneo. Compared to other primates, this value is extremely low. Where values are approaching 1, orangutans can be considered to be under high time-budgeting stress and likely to be extremely vulnerable to any further environmental degradation.

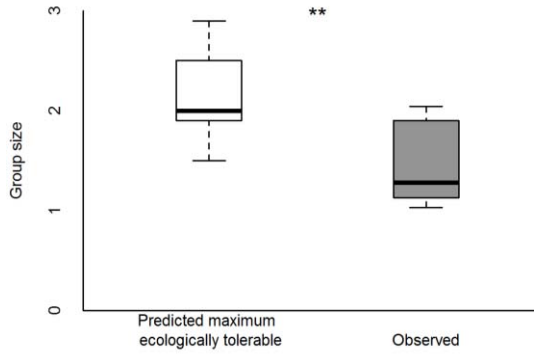


Fig. 4. Predicted maximum ecologically tolerable group sizes at the orangutan field sites in comparison to the observed values (indicates that P < 0.01).**

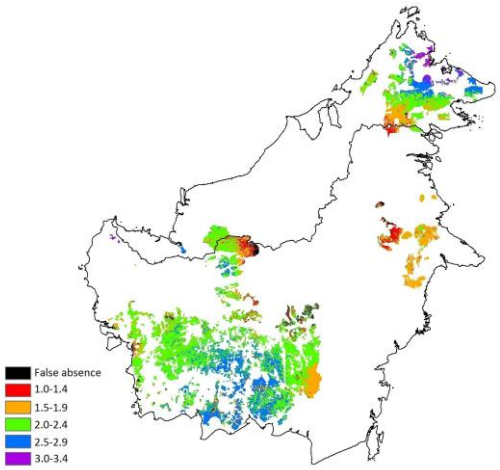


Fig. 5. Predicted maximum ecologically tolerable group size (METGS) within the current range of the orangutan in Borneo (lines indicate country boundaries); black indicates areas where the model failed to predict the actual presence of orangutans, and white areas are outside the observed range of the orangutan and so predicted METGS are not displayed. Low METGSs indicate high ecological stress in marginal habitats.

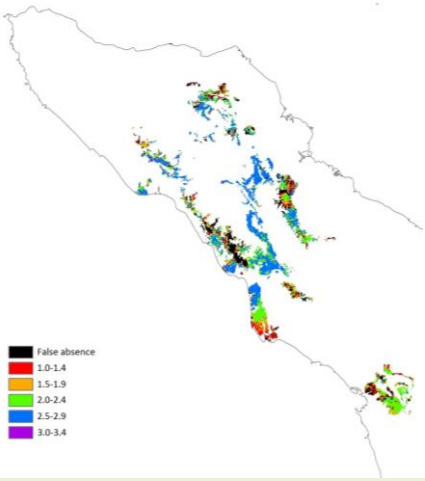


Fig. 6. Predicted maximum ecologically tolerable group size (METGS) within the current range of the orangutan in Sumatra; black indicates areas where the model failed to predict the actual presence of orangutans, and white areas are outside the observed range of the orangutan and so predicted METGS are not displayed. Low METGSs indicate high ecological stress in marginal habitats.

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Discussion

One of the major advantages of time budget models is that they can be used to investigate the factors that constrain both distribution patterns and levels of sociality [8]. Our results suggest that orangutan distribution patterns are primarily restricted by high resting time requirements in areas of low forest cover and low fruit availability. The model predictions also indicate that it is ecological constraints that constrain orangutan sociality, and suggest that the orangutan is living close to the limits of survival throughout its entire range.

Large areas of Borneo and Sumatra were predicted to be unsuitable for the orangutan, owing to low forest cover and fruit availability, as these are predicted to lead to high resting time requirements. Low forest cover may increase exposure to the sun, forcing orangutans to spend more time resting to prevent overheating [47]. In logged areas it has been shown that there are fewer large food trees [48] and that orangutans eat a higher proportion of leaves than in primary forest [49]. Similarly, in the heavily degraded habitat of Batang Serangan, orangutans rely heavily on bark [50], while orangutans living in acacia plantations also seem to obtain a large proportion of their energy from cambium [51]. This suggests that areas with reduced forest cover may provide fewer fruit resources for orangutans, preventing their habitation by forcing them to rely heavily on fallback foods, which incur high resting time demands. Gorilla distributions have also been shown to be constrained by resting time, also interpreted as a result of increased reliance on fallback foods such as leaves and bark in more marginal habitats [7]. This indicates a common response to habitat degradation in the two ape taxa.

Fruit availability is clearly an important determinant of habitat suitability for the orangutan, and in fact the orangutan diet may not be very flexible. Predicted values for the percentage of fruit in the diet in areas where orangutans were correctly predicted to survive were relatively clustered around the mean. This indicates that orangutans may require a threshold level of fruit in the diet, and that they may struggle to survive on a diet of less than about 40% fruit. This finding clearly emphasizes the vulnerability of the orangutan to habitat degradation, as it may have little ability to alter its diet in response to changes in habitat quality.

Korstjens et al [2010] investigated resting time in 78 genera of African and American primate species and found that they would struggle to survive in locations that required more than 33% enforced resting time. Our model suggests that orangutans, like other primates, may be restricted by a maximum value of enforced resting time, which may be preventing them from living in some of the areas that were predicted by the model to be suitable. We found that resting time was significantly higher in areas that orangutans were predicted to inhabit, but in which they are not currently recorded to live, than in locations that were correctly predicted to be unsuitable. This implies that, in line with Korstjens et al [2010], there is a maximum amount of time that orangutans can realistically devote to enforced resting, above which they cannot survive, and this amount appears to be in the region of 30-40% of time.

In contrast to the resting time results, moving time does not appear to be a restrictive factor for orangutans. Moving time was significantly higher in locations that were correctly predicted to be suitable than in locations that were incorrectly predicted to be suitable, suggesting that this is not preventing the orangutan from inhabiting these ‘false presence’ locations.

Interestingly, the results suggest that the locations that are unsuitable for habitation overall provide the ‘best’ environments in terms of feeding time, which seems counterintuitive; feeding time was found to be significantly higher in locations where the orangutan was correctly predicted to survive than in locations correctly predicted as unsuitable. This is likely due to the positive relationship between feeding time and forest cover; as forest cover increases, feeding time also increases (possibly a result of the availability of higher quality foods that require greater extraction times). Alternatively,

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low forest cover could be an indicator of agricultural areas, which provide high quality foods for orangutans (thus low feeding time), but are otherwise not suitable habitat. In addition, the results may be affected by the model extrapolating beyond the data in some places. Many of the locations with very low predicted feeding time values are in southern Sumatra, where intense deforestation has reduced forest cover to extremely low levels. This leads to very low predicted values for feeding time, which are not likely to be representative of reality. The linear relationship between feeding and forest cover is based on a sample size of 11 populations, with forest cover ranging from 33 to 80%. Although this is quite a large range, the linear equation produced cannot tell us anything about the relationship between feeding and forest cover at levels of forest cover lower than 33%, which is most likely not a continuation of this linear relationship. Therefore, calculating a value for feeding time at forest cover values of 0-10%, such as in much of southern Sumatra, is extrapolating beyond the data, and consequently may give unrealistic values. However, in terms of the overall model, this is not a problem as these locations are deemed unsuitable by both the other time budget components and by the land cover data.

The model suggests that orangutans do not have a large range of group sizes available to them and that overall sociality may be limited by ecology. All of the predicted maximum ecologically tolerable group sizes in Borneo and Sumatra were relatively low, with values of around two predicted for most of the orangutan's current range and a maximum value of only 3.4. This is interesting compared to the other species of great apes that all live in larger and more cohesive groups. Although chimpanzees have a fission-fusion social system, their average party size far exceeds that of the orangutan [29, 52-54]. For orangutans, group size was found to be a major predictor of resting time allocations, with resting time demands increasing as group size increased. This is probably due to the effect of feeding competition, which has been suggested as the major constraint on orangutan sociality [10, 12]. Fruiting trees in Southeast Asian rainforests are small and dispersed, allowing a single orangutan to consume all of the fruit from a tree in one feeding bout [14]. In larger groups there is therefore more competition for food, and fruit trees will be depleted more rapidly. As a result, orangutans may be forced to eat more fallback foods such as leaves and bark which require longer digestion times, and thus more resting time.

It is interesting that the model did not predict increases in moving and feeding time as group size increased, as these may also be expected to increase with feeding competition. The unproductive nature of the rainforests may make foraging for fallback foods a more successful strategy than searching for new fruit sources. Our study therefore indicates that the orangutan's solitary social system might be a response to the intense feeding competition that occurs in groups, imposing high resting time demands. This finding concurs with the current consensus on orangutan sociality, which attributes their asocial nature to the high ecological costs of grouping [10, 12].

Finally, it has been suggested that if habitat quality declines, primates can sometimes respond by reducing their group size, thereby reducing the time required for social activities [55]. This extra time can then be used for other more critical activities. A smaller group size also has lower levels of feeding competition, and therefore potentially less time is required for feeding and moving [55]. This ability to reduce group size has been termed social flexibility [55]. Orangutans clearly have an extremely limited ability to adapt in this way, as they are already approaching the limits of group size. Populations living close to the limits of group size are predicted to be under high levels of time budgeting stress, as they have little time that is not committed to activities essential for survival. It is clear that the populations in eastern Borneo, as well as in a few patches in northern and central Borneo, are under considerable time budgeting stress, as their maximum predicted ecologically tolerable group sizes are close to 1. This means that they are extremely vulnerable to habitat changes that could lead to increases in time budget allocations. Overall, maximum group sizes predicted by the model are relatively low in the entire range of the orangutan, which indicates that even in prime habitat,

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orangutans do not have a great deal of social flexibility available to them. Therefore, even in the best habitats, orangutans are unlikely to be able to withstand much environmental damage.

Implications for Conservation

Our study highlights the extremely vulnerable position of the two orangutan species. We provide evidence that especially high resting time demands, related to diet and forest cover, prevent the orangutan from living in much of Borneo and Sumatra, including many regions that made up parts of its previous range. Orangutans appear to have limited dietary and social flexibility, which leaves them poorly equipped to adapt to further environmental disturbances. In many regions, predicted maximum ecologically tolerable group sizes approach the minimum possible value, suggesting that in these areas, the orangutan is particularly vulnerable to extinction. It should be recognized that the time budget model described here does not take into account potential behavioral adaptations to environmental changes. Orangutans in north-east Borneo, for example, have been observed to adopt more terrestrial behavior in recently logged areas [68]. Orangutans may also be more resilient to conversion to plantations than previously assumed, with recent evidence suggesting that they can survive in acacia plantations [69]. Thus it is possible that orangutans will be able to adapt to these changes to their habitat. However, the results of our study clearly highlight that the orangutan is living close to the limits of what is ecologically possible throughout its entire range and thus how essential it will be to protect their habitat, even if they can adapt in certain ways to the impacts of human activities.

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