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The Effects of Climate Change on Orangutans: A Time Budget Model

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1. Introduction

The investigation of the potential effects of climate change on species distributions is a major focus of conservation biology (Guisan & Thuiller, 2005; Sinclair et al., 2010). Numerous predictive models have been developed, the majority of which utilise correlations between the observed distribution of a species and climate variables to produce a 'climate envelope' in which the species is predicted to live (Pearson & Dawson, 2003). However, these models provide little insight into the mechanisms that determine distributions or the effect that climate change will have on behaviour (Lehmann et al., 2010). Time budget models have been developed that incorporate behaviour as an intermediate link between climate and survival, allowing for a more in depth analysis of the factors that limit distribution patterns. These models can identify probable future distributions, and predict the potential effects of climate change on behaviour and sociality (see Dunbar et al., 2009 for a review). The basic assumption of these models is that time is an important constraint that can affect a species' ability to survive in a given habitat. Theoretically it is always possible for an individual to meet its nutritional requirements regardless of food quality, provided that there is sufficient time available to find, ingest and digest an adequate amount of forage (Dunbar et al., 2009). Thus, it is essentially time that constrains the animal's ability to survive. For an animal to survive in a given location it is therefore vital that it can perform all of its essential activities within the time available (Dunbar, 1992). Time constraints are clearly important factors that are overlooked by the more conventional species distribution models.

In this chapter we use a time budget model to examine orangutan distribution patterns under future climate change scenarios. There are two species of orangutan currently recognised, *Pongo pygmaeus* and *Pongo abelii*, which inhabit the islands of Borneo and Sumatra respectively (Goossens et al., 2009). Both species of orangutan are endangered; in 2004 only 6,500 Sumatran orangutans and 54,000 Bornean orangutans were estimated to remain in the wild (Wich et al., 2008). Orangutans are large-bodied arboreal great apes, with a primarily frugivorous diet (Morrogh-Bernard et al., 2009). Although orangutans spend the majority of their time alone, they have been shown to form clusters with neighbouring individuals and can therefore be viewed as social animals (Singleton & van Schaik, 2002). Orangutans are characterised by slow life histories with long maturation rates and interbirth intervals (Delgado & van Schaik, 2000; Wich et al., 2009). This makes them particularly vulnerable to extinction (Cardillo et al., 2004), as populations can take many years to recover

from loss of individuals for example due to hunting (Singleton et al., 2004). Great apes in general are also particularly threatened by habitat loss from deforestation, as a result of their large home range and dietary requirements (Campbell-Smith et al., 2011). The effects of further habitat loss due to future climatic change could therefore have a considerable impact on the survival chances of the orangutan. The investigation of the effect of climate change on the range of the orangutan could provide valuable information for the conservation of these two endangered species.

Previous work on the effects of climate change on primate distribution patterns has shown that climate change is likely to significantly reduce the range of both gelada baboons (Dunbar, 1998) and the African great apes (Lehmann et al., 2010). Because time budget models utilise existing relationships between climatic, dietary and demographic variables and their effects on behaviour, they can be used to predict the amount of time that animals would need to devote to each activity under different climate scenarios. The climate affects individual behaviour 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. In addition, because most primates are social, the size of the social group needs to be factored in to the models. Group size can affect time budgets through food competition, leading to an increase in feeding, moving or resting time (Dunbar, 1996), as well as through the need to maintain social relationships via grooming (Lehmann et al., 2007), which in large groups can take up a substantial amount of time. Time budget models take these effects into account and allow us to determine not only the presence or absence of a species in a habitat, but also to calculate the group sizes at which it could persist in a given location. The group size at which all available time has been allocated to time budget demands is the maximum ecologically tolerable group size that can be adopted in a specific location (Dunbar, 1992).

Time budget models therefore provide advantages over the correlative approach of bioclimate envelope models. Time budget models have been shown to predict species distributions as accurately as climate envelope models (Korstjens & Dunbar, 2007; Willems & Hill, 2009), but can also be used to understand the mechanisms that determine distributions, both now and in the future, as well as potential impacts on behaviour (Dunbar et al., 2009; Lehmann et al., 2010). Time budget models have been created for three species of great apes to date: gorillas, chimpanzees and bonobos (Lehmann et al., 2008a, 2008b, 2010; Lehmann & Dunbar, 2009). In this chapter we investigate the potential effects of climatic change on orangutan distribution patterns using a time budget model. Anthropogenic effects such as deforestation and hunting have a considerable impact on the distribution of the orangutan (Rijksen & Meijaard, 1999); therefore we also incorporate land cover and human population density data into the model.

2. Methods

2.1 Overview

Regression equations were created to predict the amount of time that orangutans ought to devote to each of the time budget variables from climatic, dietary and demographic data. Using raster data in ArcGIS 9.3, time budget allocations were predicted across Borneo and Sumatra, and summed to calculate the maximum ecologically tolerable group size of the

orangutan across the islands. This was combined with land cover and human population density data to create a presence/absence map for the orangutan. The model was then re-run using a number of future climate projections to predict the effect of climate change on the distribution of the orangutan.

2.2 Data collection

Data were collected from published studies to compile a dataset of orangutan time budgets (time spent feeding, moving and resting), diet (percentage of feeding time spent eating fruit and leaves) and group size. Data were collected from 13 different orangutan study sites in total, with time budget data available for 12 of the sites (Table 1).

Climate data were obtained from Worldclim (http://www.worldclim.org/) and are displayed in Table 2. Worldclim provides a set of global climate layers for 19 bioclimatic variables at a resolution of 30 arc seconds. These layers were generated through interpolation of average monthly climate data from weather stations across the world, from 1950-2000 (Hijmans et al., 2005). All 19 variables were used in the equation finding process. The percentage of forest cover data, displayed in Table 2, were obtained from the Advanced Very High Resolution Radiometer (AVHRR) satellite data (DeFries et al., 2000; http://glcf.umd.edu/data/treecover/).

2.3 Model components

The main components of the model are diet, group size and time budgets. In addition, we included anthropogenic effects as present day primate distributions are heavily affected by human activities, such as deforestation, land cover changes and human population densities, which are not reflected in the climate data.

The orangutan diet is composed mainly of fruit and leaves (Morrogh-Bernard et al., 2009; Russon et al., 2009), which make up more than 80% of their feeding time (see Table 1); thus only these two food categories were included in the model. These variables were measured as the percentage of feeding time spent consuming fruit and leaves, which were assumed to be mutually exclusive. Diet was assumed to be influenced by the climate and the percentage of forest cover.

The majority of the orangutan's time is spent in four essential behaviours, treated here as mutually exclusive: feeding, moving, resting and socialising. Resting time is included as a key time budget variable as it is assumed to represent time that the animals are forced to devote to resting, as a result of thermoregulation and digestion demands. Feeding, moving and resting time allocations were assumed to be affected by the climate, percentage forest cover, diet and group size. Although orangutans spend the majority of their time alone, they form relationships with neighbouring individuals (Singleton & van Schaik, 2002); therefore grooming time was also included in the model, as grooming is seen as an activity that bonds individuals together. Grooming time was estimated from a generic equation calculated by Lehmann et al (2007) that determines the amount of time that individuals ought to devote to grooming to maintain group cohesion in a group of a particular size. This equation is based on the observation that grooming time in primates increases as group size increases, a result of the increased time required for maintaining relationships and group cohesion (Lehmann et al., 2007)

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Site	Latitude	Longitude	Island	Species/subspecies	Group Size	%Feeding	%Moving
Danum[1]	5.02	117.75	Borneo	*P. pygmaeus morio*	-	47.2	16.9
Kinabatangan[2]	5.53	118.28	Borneo	*P. pygmaeus morio*	-	34.1	10.3
Mentoko[3]	0.40	117.27	Borneo	*P. pygmaeus morio*	1.28	45.2	10.4
Ulu Segama[4]	5.07	117.80	Borneo	*P. pygmaeus morio*	1.93	32.3	16.4
Sabangau[5]	-2.32	113.90	Borneo	*P. pygmaeus wurmbii*	-	61.3	15.9
Cabang Panti[6]	-1.22	110.12	Borneo	*P. pygmaeus wurmbii*	1.04	36.1	9.9
Tanjung Puting[7]	-2.75	111.95	Borneo	*P. pygmaeus wurmbii*	1.18	60.1	18.7
Tuanan[8]	-2.15	114.43	Borneo	*P. pygmaeus wurmbii*	1.13	50.6	16.8
Sungai Lading[9]	-2.25	114.37	Borneo	*P. pygmaeus wurmbii*	1.03	-	-
Batang Seragan[10]	3.73	98.19	Sumatra	*P. abelii*	-	24.0	15.0
Ketambe[11]	3.68	97.65	Sumatra	*P. abelii*	2.04	48.2	12.8
Ranun[12]	3.25	97.92	Sumatra	*P. abelii*	1.85	44.1	16.0
Suaq Balimbing[13]	3.07	97.43	Sumatra	*P. abelii*	1.90	53.1	17.3

Table 1. Orangutan study sites and their locations (latitude, longitude and island), with the species/s
behavioural data (group size, feeding, moving and resting time) and dietary data (% fruit and leaves
equation finding process. Averages were used when data from more than one study were available f
site is only represented once in the dataset. Behavioural data were taken from: 1 Kanamori et al., 201
2009; 3 Mitani, 1989, 1990; Rodman, 1973, 1979; 4 Mackinnon, 1974; 5 Morrogh-Bernard et al., 2009; 6
Bernard et al., 2009; van Schaik, 1999; 7 Galdikas, 1984, 1988; 8 Bastian et al., 2010; Morrogh-Bernard
2010; 10 Campbell-Smith, 2010; Campbell-Smith et al., 2011; [11] Sugardjito et al., 1987; van Schaik, 199
Mackinnon, 1974; [13] Fox et al., 2004; van Schaik, 1999

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		Climate Variables												
Site	**Forest (%)**	**T_a**	**T_d**	**T_i**	**T_s**	**T_x**	**T_m**	**T_r**	**T_{we}**	**T_{dr}**	**T_{wa}**	**T_c**	**P_a**	**P_w**
Danum	80	26.1	7.6	8.7	36.4	30.7	22.0	8.7	25.7	25.9	26.5	25.5	2386	264
Kinabatangan	64	27.0	7.9	8.5	46.8	32.0	22.8	9.2	26.3	27.3	27.5	26.3	2711	362
Mentoko	80	26.1	7.0	8.8	23.7	30.2	22.3	7.9	26.2	25.9	26.3	25.9	1973	228
Ulu Segama	72	26.3	7.7	8.7	37.1	31.0	22.2	8.8	25.9	26.5	26.7	25.7	2416	275
Sabangau	79	26.6	8.2	8.6	36.8	31.8	22.3	9.5	26.1	26.9	27.0	26.1	2579	294
Cabang Panti	52	25.3	8.6	9.1	31.0	30.2	20.8	9.4	24.8	25.4	25.5	24.8	3258	364
Tanjung Puting	80	26.8	8.2	8.7	35.9	31.9	22.5	9.4	26.9	27.0	27.1	26.2	2723	295
Tuanan	80	26.6	8.1	8.7	30.5	31.6	22.3	9.3	26.2	26.8	26.9	26.2	2522	285
Sungai Lading	80	26.6	8.1	8.4	35.0	31.8	22.2	9.6	26.2	26.8	27.0	26.1	2508	285
Batang Seragan	33	26.8	9.6	8.7	43.1	32.5	21.5	11.0	26.5	26.5	27.3	26.2	2608	311
Ketambe	80	24.8	9.8	8.8	38.4	30.6	19.5	11.1	24.4	24.9	25.3	24.3	2563	298
Ranun	69	24.4	9.9	8.8	38.0	30.2	19.0	11.2	24.0	24.4	24.9	23.9	2868	331
Suaq Balimbing	80	26.9	9.5	8.7	43.7	32.6	21.8	10.8	26.5	27.0	27.5	26.3	2950	344

Ta = annual mean temperature; Td = mean temperature diurnal range (mean of monthly max temp - min temp)
diurnal range/temperature annual range) * 100); Ts = temperature seasonality (standard deviation *100); Tx = m
month; Tm = minimum temperature of coldest month; Tr = temperature annual range (maximum temperature
temperature of coldest month); Twe = mean temperature of wettest quarter; Tdr = mean temperature of driest q
of warmest quarter; Tc = mean temperature of coldest quarter; Pa = annual precipitation; Pw = precipitation of
of driest month; Ps = precipitation seasonality (coefficient of variation); Pwe = precipitation of wettest quarter;
quarter; Pwa = precipitation of warmest quarter; Pc = precipitation of coldest quarter

Table 2. Forest cover and 19 climate variables at each site (Temperature variables are in ^{o}C and prec

For the other model components, bivariate Pearson correlation analyses, together with visual screening of the data, were used to identify possible linear and curvilinear relationships between the behavioural and dietary variables (Table 1) and the climate and forest cover data (Table 2). Stepwise regression analyses were then performed to obtain best-fit equations to predict the percentage of fruit in the diet, feeding, moving and resting time, using the 19 climate variables, diet and group size as possible predictor variables. Variables were only added to an equation if their inclusion could be justified using biological first principles, and if they explained a significant proportion of the variation (Dunbar, 1992). Because of the small sample size, a maximum of three predictor variables were included in the regression equations (Korstjens & Dunbar, 2007); the three variables that explained the highest proportion of the variance were selected. The predictions of the equations were constrained to within biologically realistic values, to prevent the model from producing mathematically possible, but biologically improbable results (Willems & Hill, 2009). Feeding and resting time budget allocations were constrained to a minimum value of 10% and moving time was constrained to a minimum of 5%. The percentage of time that orangutans spend feeding on fruit and leaves was constrained to values between 0 and 100%.

In addition to these core model components we also included anthropogenic effects. In the past century the total human population of Borneo and Sumatra has increased dramatically (Hirschman, 1994), leading to intense deforestation and hunting pressures (Sodhi et al., 2004). Although the percentage of forest cover, an indication of deforestation, was included in the model, the data were based on satellite imagery collected in 1992-1993 and are therefore unlikely to be representative of the current situation, especially given the extremely rapid rate of deforestation in Borneo and Sumatra - forest cover declined by 1.3% in Borneo and 2.7% in Sumatra per year between 2000 and 2010 (Miettinen et al., 2011b). In order to account for the increasing impact of anthropogenic factors on the orangutans, a recent land cover map from 2010 was incorporated into the model (Miettinen et al., 2011a; http://www.eorc.jaxa.jp/SAFE/LC_MAP/), so that areas where human induced land use changes are likely to prevent orangutans from persisting could be identified. Land cover categories were separated into those suitable for orangutans or unsuitable (Table 3).

Suitable Habitat	**Unsuitable habitat**
Mangrove	Plantation/regrowth
Peatswamp forest	Lowland mosaic
Lowland forest	Montane mosaic
Lower montane forest	Lowland open
Upper montane forest	Montane open
	Urban
	Large-scale palm plantation

Table 3. Land cover categories (suitable and unsuitable habitat) from the 2010 land cover map (Miettinen et al., 2011a).

Human population density (HPD) was also added to the model as it can be used as a summary measure of human impacts (Cardillo et al., 2004). HPD data were obtained from the Oak Ridge National Laboratory (UT-Battelle, LLC) LandScan 2008™ High Resolution Global Population Data Set (http://www.ornl.gov/sci/landscan/). In order to choose an

appropriate threshold for the value of HPD above which orangutans were unlikely to survive, the distribution of HPD values within locations in the observed orangutan range was examined. Although some locations within the orangutan range have extremely high values of HPD, this is likely to be the result of errors in estimation of either HPD or the orangutan range, both of which were determined based on relatively crude methods. A threshold of 20 people per square kilometre was chosen as an appropriate threshold as almost 97% of locations within the orangutan range were characterised by HPD values lower than this threshold (Table 4). In addition, increasing the threshold above 20 people per square kilometre leads to relatively small increases in the percentage of locations with HPD values below the threshold, while decreasing the threshold below 20 leads to increasingly large decreases in this percentage. This indicates that orangutans may struggle to survive in locations with HPD above 20 people per square kilometre.

Threshold value of HPD (people per km^2)	Proportion of range with HPD < threshold
30	97.7
25	97.3
20	96.8
15	95.2
10	92.7
5	86.3

Table 4. The proportion of the current orangutan range with human population densities (HPD) below different threshold values.

2.4 Model procedure

The equations were implemented in ArcGIS version 9.3 to predict time budget allocations of orangutans for each pixel in a raster image across Borneo and Sumatra. The maximum ecologically tolerable group size was determined by calculating the sum of the time budget allocations for each pixel. Group size was then increased algorithmically from 1, until the total time budget allocations exceeded 100%. The maximum ecologically tolerable group size is defined as the group size of the previous iteration. Although orangutans have been shown to form clusters with neighbouring individuals (Singleton et al., 2009; Singleton & van Schaik, 2002), they spend the majority of their time alone (Bastian et al., 2010; Galdikas et al., 1981; van Schaik, 1999); therefore they are assumed to be able to survive in a location if the predicted maximum group size is greater than or equal to 1. Thus, the orangutan is predicted to be able to survive in all pixels with a predicted maximum ecologically tolerable group size greater than or equal to 1, a suitable land cover category and a HPD value less than 20 people per square kilometre.

2.5 Validating the model

The model was validated in three ways. Firstly, the predicted distribution was compared against the observed range of the orangutan, to determine how accurately the model predicted the current distribution. The observed distribution was obtained from UNEP-WCMC (Meijaard et al., 2004) and was based on extensive ground and aerial surveys and forest data from both satellite imagery and the Indonesian Ministry of Forestry (Wich et al.,

2008). Secondly, predicted values for orangutan maximum ecologically tolerable group size were compared with observed values from the 9 sites for which there were data. Observed group sizes should fall equal to or below the predicted maximum values. Observed and predicted group sizes were compared using Wilcoxon signed-ranks tests. Finally, sensitivity analyses were used to evaluate the robustness of the model to errors in parameter estimates. The parameter estimates in the regression equations were each changed one at a time by +5%, -5%, +50% or -50% and the model re-run. All parameters were then changed simultaneously by +5%, -5%, +50% or -50% and the four resulting models run. The predictions of the altered models were compared to the predictions of the original model to determine the sensitivity of the model to error. Ideally, the model should be robust to small changes in parameter estimates (~5%) but sensitive to large changes (~50%). Comparing the predictions for every pixel in the raster image is problematic as the pixels are not independent; therefore a grid consisting of 374 locations across Borneo and Sumatra separated by 0.5° longitude and latitude was created. The prediction (i.e. presence or absence) at each of these locations was extracted for the original model and all sensitivity analysis models for comparison. This improves the independence of the data compared to pixel level resolution and thereby allows the predictions of the altered models to be compared with those of the original model. Chi-squared tests were used to determine if the altered equations produced significantly different results from the original model. All statistical analyses were performed in SPSS version 17.

2.6 Climate change and human population growth effects

In order to assess the effects of climate change on the biogeographical range of orangutans, the model was re-run using predicted future scenarios. All analyses were restricted to the orangutan's current distribution; therefore we did not consider range increases, as it is assumed that anthropogenic factors would prevent any future expansions. Predicted climate data for 2080 (the date furthest in the future for which data are available) were downloaded from the International Centre for Tropical Agriculture (Ramirez & Jarvis, 2008; http://ccafs-climate.org/). The data had been statistically downscaled using the delta method (Ramirez & Jarvis, 2010). Two future emissions scenarios were chosen (SRES A2a and SRES B2a), representing alternative predictions for the future. The A2a scenario is characterised by high energy requirements and continuous human population growth, while the B2a scenario is based on assumptions of lower energy requirements and slower population growth (Nakicenovic et al., 2000). Within these scenarios, data were available from four different and widely used Global Circulation Models (CCCMA-CGCM2 (hereafter CCCMA), CSIRO-MK2 (hereafter CSIRO), NIES99 and HACCPR HadCM3 (hereafter HadCM3)) for each of the two scenarios. Data were obtained for all four models in order to examine a range of future predictions (Jenkins et al., 2011). The models produce predictions at very coarse resolutions (CCCMA = 3.7° by 3.7°; CSIRO = 5.6° by 3.2°; HadCM3 = 2.5° by 3.8°; NIES99 = 5.6° by 2.8°), therefore statistically downscaled data were used to increase the resolution of the data. All models predict warming climates, while predictions for precipitation vary, with CCCMA predicting a decrease in annual rainfall across Borneo and Sumatra and the other three models predicting increases (Table 5).

	Change in mean annual temperature (°C)		Change in mean annual precipitation (mm)	
	A2a	**B2a**	**A2a**	**B2a**
CCCMA	+ 2.51	+ 1.60	- 197.12	- 143.46
CSIRO	+ 3.20	+ 1.99	+ 352.17	+ 270.65
HadCM3	+ 3.47	+ 3.04	+ 183.40	+ 176.24
NIES99	+ 3.48	+ 2.19	+ 288.23	+ 88.68

Table 5. Changes in mean annual temperature and precipitation predicted for 2080 across Borneo and Sumatra under the 8 combinations of 4 climate models and 2 emissions scenarios.

The time budget model was re-run using future climate data from all four models (CCCMA, CSIRO, NIES99 and HadCM3) under both emissions scenarios (SRES A2a and B2a). Because we know very little about the effect of climate change on tropical forests (Clark, 2004), forest cover was assumed to remain constant. Similarly, land cover data were maintained as in the original model, as it is impossible to predict these changes. The human population density in 2080 across the region was predicted by calculating the percentage increase in global population from 2008 to 2080 predicted by the two emissions scenarios. The population density of each pixel was then increased by the same percentage (an increase of 98% under the A2a scenario and 43% under the B2a scenario).

3. Results

3.1 Equations

The regression equations obtained are presented in Table 6 and summarised in Figure 1. In addition to the equations for feeding, moving and resting time, a regression equation was produced for the percentage of fruit in the diet from which the percentage of leaves in the diet can be calculated, as this variable was a significant predictor of feeding time.

Variable	Equation	R^2adj	N	F	P
Feeding	22.081 + 0.665*Forest – 0.806*Leaves – 0.032*Precipitation of Wettest Month	0.91	11	35.99	<0.001
Moving	-97.085 + 0.358*Temperature Seasonality – 0.0005*Temperature Seasonality ^{2} + 0.189*Mean Temperature of Wettest Quarter	0.56	12	5.61	<0.05
Resting	128.548 + 27.417*Group Size – 0.968*Forest – 0.176* Temperature Seasonality	0.88	8	17.58	<0.01
Fruit	174.100 – 0.488* Precipitation of Warmest Quarter + 0.0004* Precipitation of Warmest Quarter ^{2} + 0.267*Forest	0.56	13	6.06	<0.05
Leaves	100 - Fruit				
Social	1.01 + 0.23*Group Size	Generic equation†			

† Equation from Lehmann et al, 2007

Table 6. Multiple regression equations for time budget and diet variables, with the adjusted R^2, the sample size, and the significance of the equation.

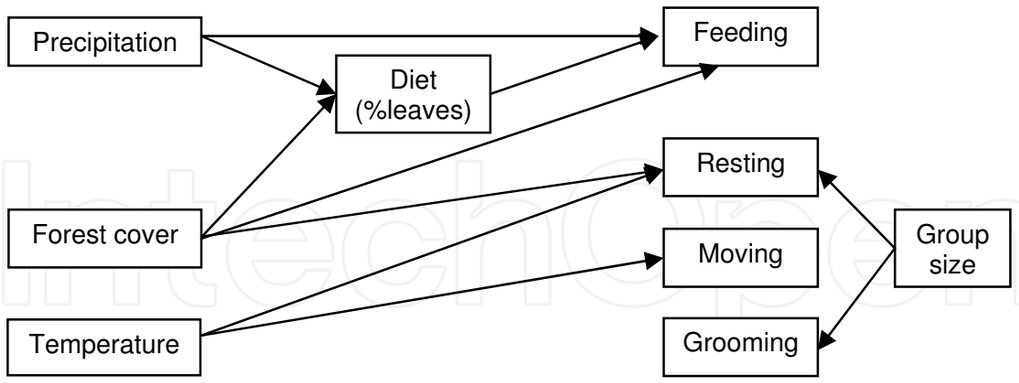


Fig. 1. Flow chart depicting relationships between climate and forest cover variables and the time budget components. The arrows indicate directional relationships used in the model.

The equations highlight the important effect of forest cover on time budget allocations. The positive relationship between forest cover and fruit could be the result of a higher availability of fruit in dense forest than in more degraded habitats. Forest cover also predicted feeding and moving time, and it is likely that these relationships reflect the effect of forest cover on diet. In densely forested areas orangutans may need to spend less time resting and more time feeding, possibly as a result of the increased availability of high quality food that requires less time for digestion but more time for extraction (which would be attributed to feeding time). In contrast, in more sparse forests, orangutans may be forced to rest more to conserve energy (and to digest the higher percentage of leaves in their diet) and feed less. Resting time was also affected by group size and temperature seasonality. As group size increases fruit sources will be depleted faster and orangutans may be forced to consume more leaves which require more digestion time. The relationship with temperature seasonality indicates that orangutans spend more time resting in areas with more consistent temperatures. This may reflect higher resting time requirements in areas closer to the equator, where temperatures are higher and less variable (Chuan, 2005). When temperatures are high animals are unable to perform many of their essential activities, and are thus forced to rest (Korstjens et al., 2010).

Feeding time was negatively related to the amount of leaves in the diet. Similarly, among the African great apes, it was found that feeding time increased as the percentage of fruit in the diet increased (Lehmann et al., 2008b). These relationships may reflect the reduced foraging and processing times required to eat leaves.

3.2 Model validation

The current range of the orangutan is displayed in Figure 2.

The model produced a presence/absence map for the orangutan. This was compared against the observed distribution (Figure 3).

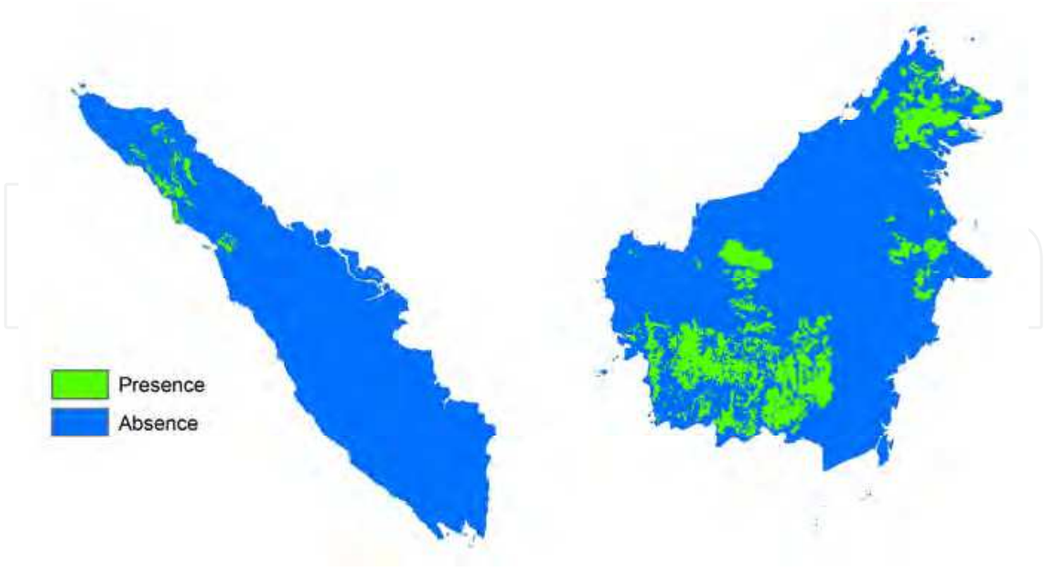


Fig. 2. The current distribution of the orangutan (Meijaard et al., 2004).

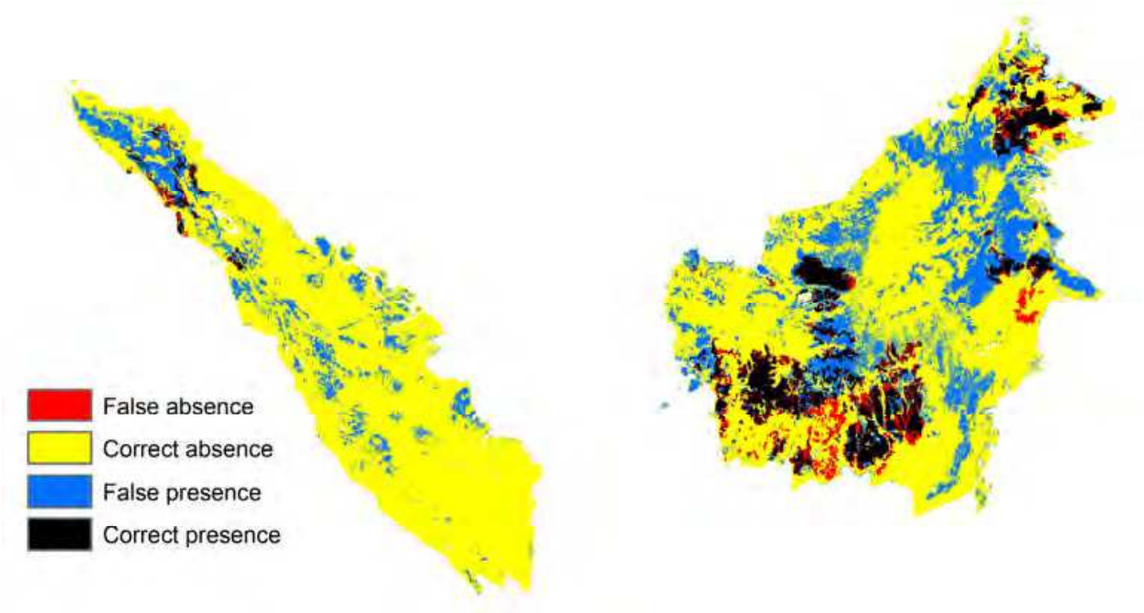


Fig. 3. Predicted distribution of the orangutan based on the model compared against the observed distribution. False absences indicate locations where orangutans are present but the model predicted absence, correct absences are locations where orangutans are absent and the model predicted absence, false 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.

Overall, the model correctly predicted the presence or absence of orangutans in 77.0% of raster pixels. The model correctly predicted orangutan absence from 78.1% of the areas from which they are currently thought to be absent and correctly predicted their presence in 68.3% of their current range (Table 7). The number of correct predictions (when analysed across the grid of 374 points) is significantly higher than would be expected by chance, based on the observed proportion of presences and absences ($\chi^2 = 11.87$, df = 1, N = 374, P < 0.001).

		Observed	
		Present	**Absent**
Predicted	**Present**	68.3	21.9
	Absent	31.7	78.1
	Total	100	100

Table 7. Table of model performance, displaying the percentage of observed presences and absences that were predicted to be presences and absences.

The model therefore incorrectly predicted the presence or absence of orangutans in just over 20% of raster pixels. The majority of these false predictions were those where the model predicted suitable habitat for orangutans but no orangutans were recorded to live there in 2007, i.e. the model overestimated the current orangutan range. To investigate this further, an orangutan distribution map was obtained for the island of Borneo from 1930 (Rijksen & Meijaard, 1999), and compared with the model predictions for Borneo. This showed that 45.2% of these false presences are in land that was previously suitable for orangutans according to the 1930 map, thereby confirming that climatically these areas may be suitable.

Similarly, 58.3% of those locations that were incorrectly identified as unsuitable for orangutans by the model were in areas that are now classified as plantations or regrowth in the 2010 land cover map, and were thus classed as unsuitable for orangutans. This conversion to plantations appears to be relatively recent, as 75.2% of the locations classified as plantations in 2010 were classed as forested in a land cover map from 2000 (Global Land Cover 2000, 2003; http://bioval.jrc.ec.europa.eu/products/glc2000/glc2000.php).

Observed group sizes were compared against the maximum ecologically tolerable group sizes predicted by the model. Observed group sizes should be less than or equal to the maximum ecologically tolerable group size; figure 4 shows that this is the case for all of the points. Predicted maximum ecologically tolerable group sizes are significantly higher than observed group sizes (WSR: Z = -2.668, N = 9, P < 0.01), and still within a realistic range of the observed grouping patterns (Figure 4).

Sensitivity analyses were performed to determine the robustness of the model to errors in parameter estimates. Changes of 5% resulted in presence/absence distributions that were significantly different from the original model in only 1 of 36 runs, while changes of 50% led to significantly different distributions in 21 of 36 runs (all $\chi^2 > 3.84$, df = 1, N = 374, P < 0.05). Thus, the model is robust to small errors and sensitive to large errors in parameter estimates. Changing all parameters at once by both ±5% and ±50% led to significantly different presence/absence distributions than the original model in all four runs (all $\chi^2 > 11$, df = 1, N = 374, P < 0.001). This indicates that it is the particular set of parameter values obtained that is important.

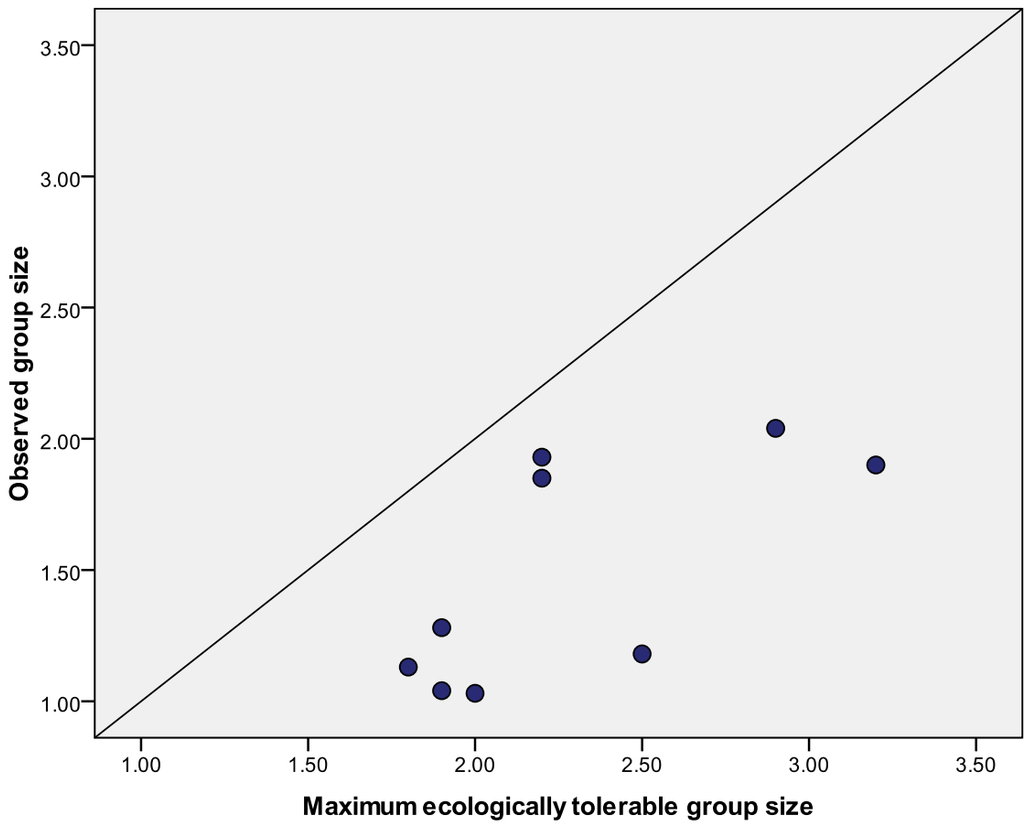


Fig. 4. Observed group sizes versus predicted maximum ecologically tolerable group sizes (the line of equality is the line on which the maximum ecologically tolerable group size equals the observed group size).

3.3 The effect of climate change and human population growth

3.3.1 Biogeography

The percentage of the orangutan's current range that is predicted to become unsuitable as a result of climate change and human population growth was calculated (the areas classed as false absences in the original model were excluded) (Table 8). The majority of the models predict that the orangutan will lose approximately 5% of its current range under scenario A2a and around 3% under scenario B2a. However, the CSIRO model predicts a larger reduction in the suitable range of the orangutan, by just over 15% under scenario A2a and 13% under scenario B2a.

	A2a	**B2a**
CCCMA	5.11	3.28
CSIRO	15.34	13.43
HadCM3	4.83	3.35
NIES99	6.61	3.05

Table 8. The percentage of the orangutans' current range that is predicted to be lost as a result of climate change and human population growth under the 8 combinations of 4 climate models and 2 emissions scenarios.

The CSIRO model thus produces a much larger range reduction than the other three models under both scenarios. A particular strength of time budget models is that they allow us to investigate in greater detail what exactly it is that is making this habitat unsuitable for orangutans, i.e. we can investigate the mechanisms underlying the range reduction. Mean time budget values were obtained for the locations predicted to become unsuitable under the CSIRO model, and compared with the mean value at these sites under the original model. The mean value for feeding time increased considerably by 2080 under both scenarios, with moving time increasing to a lesser degree and resting time changing very little ($Mean_{A2a}$: Feeding = 47.57 versus 30.24, Moving = 14.10 versus 10.26, Resting = 33.64 versus 33.22; $Mean_{B2a}$: Feeding = 51.84 versus 30.81, Moving = 14.44 versus 10.94, Resting = 31.77 versus 31.94).

3.3.2 Group size

Group size estimates were compared within the locations where the orangutans are predicted to survive under both current and future climates. For each model/emissions scenario combination as well as the original model, predicted values were obtained for all points on the grid in which the orangutan was predicted to survive under both climatic conditions. These values were compared to determine the effect of climate change on grouping patterns. All of the models except CSIRO predicted either no significant change or an increase in the maximum ecologically tolerable group size (Table 9). The CSIRO model predicts a decrease in the maximum ecologically tolerable group size in the future.

	A2a				**B2a**			
	Direction	**Z**	**N**	**P**	**Direction**	**Z**	**N**	**P**
CCCMA	NS	-1.000	24	0.317	NS	-1.342	24	0.180
CSIRO	Decrease	-2.000	20	< 0.05	Decrease	-2.646	21	< 0.01
HadCM3	Increase	-2.646	24	< 0.01	Increase	-2.646	24	< 0.01
NIES99	NS	-1.342	24	0.180	Increase	-2.121	24	< 0.05

Table 9. Results of Wilcoxon signed-ranks tests, indicating the direction and significance of predicted changes to the maximum ecologically tolerable group size within locations in which the orangutan is predicted to survive under both current and future conditions, for all 8 combinations of the 4 climate models and 2 emissions scenarios (NS = not significant).

3.3.3 Time budgets

Time budget estimates were also obtained for each of the locations in the grid in which the orangutan was predicted to survive under both climatic conditions, to compare current and future values. The predicted changes to time budget allocations are displayed in Table 10.

The NIES99 model and the CSIRO model predict that feeding will only increase significantly under the B2a scenario. The other model/scenario combinations predict no significant change. Moving time is predicted to increase under both scenarios by the CCCMA and CSIRO models, and under the A2a scenario by the NIES99 model. The CCCMA, HadCM3 and NIES99 models all predict a decrease in resting time under both possible futures, while the CSIRO model predicts no significant change.

		A2a				B2a			
		Direction	**Z**	**N**	**P**	**Direction**	**Z**	**N**	**P**
Feeding	**CCCMA**	NS	-0.983	24	0.326	NS	-0.522	24	0.602
	CSIRO	NS	-0.742	20	0.458	Increase	-2.185	21	< 0.05
	HadCM3	NS	-0.524	24	0.600	NS	-0.403	24	0.687
	NIES99	NS	-1.689	24	0.091	Increase	-2.142	24	< 0.05
Moving	**CCCMA**	Increase	-2.621	24	< 0.01	Increase	-2.560	24	< 0.05
	CSIRO	Increase	-4.054	20	< 0.001	Increase	-4.055	21	< 0.001
	HadCM3	NS	-0.017	24	0.986	NS	-0.281	24	0.779
	NIES99	Increase	-4.082	24	< 0.001	NS	-0.137	24	0.891
Resting	**CCCMA**	Decrease	-3.662	24	< 0.001	Decrease	-2.784	24	< 0.01
	CSIRO	NS	-0.829	20	0.407	NS	-1.269	21	0.204
	HadCM3	Decrease	-4.018	24	< 0.001	Decrease	-3.949	24	< 0.001
	NIES99	Decrease	-3.742	24	< 0.001	Decrease	-4.019	24	< 0.001

Table 10. Results of Wilcoxon signed-ranks tests, indicating the direction and significance of the predicted changes to time budget allocations within locations in which the orangutan is predicted to survive under both current and future conditions, for all 8 combinations of the 4 climate models and 2 emissions scenarios (NS = not significant).

4. Discussion

4.1 Overview

Time budget models have previously been shown to produce species distribution maps comparable in accuracy to climate envelope models (Korstjens & Dunbar, 2007; Willems & Hill, 2009). In addition, time budget models can also be used to assess the effects of changes in the climate on individual behaviour, diet and group sizes, helping us to understand what exactly is causing the changes in biogeography. In this study, we found that only one of the scenarios tested predicted a substantial change in orangutan distribution by 2080, while a relatively mild effect on the range of the orangutan was found for the remaining three models, which predicted a reduction of between 3 and 7%. However, given the additional pressures of deforestation and hunting by humans, this reduction could have a severe impact on the survival of the species.

4.2 Model performance

Although the model predicts the overall distribution of the orangutan encouragingly accurately, it tended to overestimate orangutan ranges in certain areas, i.e. the model identified habitats as climatically suitable for the orangutan where they are not currently recorded to live. A number of possible reasons may help to explain these deviations. Firstly, areas may indeed be suitable, but dispersal barriers have prevented the orangutan from colonising them. In the south-east of Borneo, for example, the Barito and Mahakam rivers may have prevented the orangutan from entering this region, as orangutans are unlikely to attempt to cross wide rivers with fast flowing water (Rijksen & Meijaard, 1999). Secondly, although we included some anthropogenic factors in the model, some effects such as hunting by small-scale societies were not included. Archaeological evidence indicates that orangutans have been hunted for thousands of years by the indigenous people of both

Borneo and Sumatra (Harrison, 2000; Rijksen & Meijaard, 1999). It has been suggested that the absence of the orangutan from areas in northern Borneo is the result of past hunting by indigenous people (Rijksen & Meijaard, 1999) while the areas where sizeable populations remain in Borneo are those inhabited by Muslim groups, who for religious reasons do not hunt the orangutan (Sugardjito, 1995). Thus, many of the locations predicted as suitable where the orangutan is not recorded to live, particularly those in northern Borneo, may be climatically suitable areas for the orangutans but represent locations where they have been extirpated by prehistoric human populations. Hunting by contemporary populations may also explain the absence of orangutans from otherwise suitable areas. Marshall et al (2006) found that the distance to the nearest village known to hunt orangutans was the most important predictor of orangutan density in East Kalimantan. Orangutans have an extremely slow reproductive rate (Knott et al., 2009; Wich et al., 2009) and therefore even relatively mild hunting pressures can have dramatic effects on orangutan population sizes (Marshall et al., 2009; Singleton et al., 2004). Thus, both past and current hunting pressures can significantly impact on the distribution of the orangutan, and may explain why orangutans were not found to live in some of the areas in which they are predicted to be able to survive. Although the model included human population density in an attempt to account for such human effects, hunting of orangutans is often performed by small groups of indigenous people that are unlikely to be characterised by high population densities.

Many of the locations in which the orangutan is absent but the model predicted them to live were those adjacent to its current range. The range of the orangutan has contracted dramatically in the past century, and has become increasingly fragmented (Husson et al., 2009). The estimated distribution of the orangutan in 1930 indicates that it once ranged much more continuously across southern Borneo and along the eastern coast (Rijksen & Meijaard, 1999). In Borneo, 45.2% of the locations incorrectly predicted as suitable habitat are within the orangutan's 1930 range. These areas may therefore be climatically suitable, but uninhabited by orangutans as a result of recent anthropogenic effects not incorporated in the model.

Another problem that causes inaccuracies in any kind of climate model is the limited availability of accurate and recent data on distribution patterns, land cover and climate. Although we were able to use a very recent land cover map in the current study, orangutan distribution patterns were based on data from 2007, while climate data were from long-term averages over a period of 50 years. Thus, changes in climate related to land cover changes are unlikely to be reflected in the climate data. Recent orangutan distribution shifts in response to land cover change are also not recorded. These effects may at least partially explain some of the inaccuracies in the model.

Finally, the model predicted orangutans to be absent from a number of locations where they were recorded to be present in 2007. These were primarily in locations adjacent to those known to contain orangutans. The distribution of orangutans is often extremely patchy, with densities varying spatially and temporally in accordance with food availability (McConkey, 2005). Thus, there are likely to be areas that do not clearly fit into a strict definition of presence or absence, for example, those used by roaming males (Husson et al., 2009). This may explain why orangutans have been observed in areas in which the model

did not predict them to be able to subsist. This is supported by the fact that 58.3% of these 'false absences' were in pixels categorised as plantations or regrowth in the land cover map, and are therefore unlikely to support breeding populations, but may be used irregularly by orangutans with ranges on the borders of the forests. In addition, these areas may represent locations that have been converted to plantations since the orangutan distribution data were collected. Indeed 75.2% of these plantations were categorised as forest in 2000. Forest cover in South-East Asia declines by around 1% per year (Miettinen et al., 2011b), and much of the 2007 range may therefore now be unsuitable for the orangutan.

4.3 The effect of climate change and human population growth on the orangutan

Under most of the scenarios used climate change and human population growth are predicted to have a relatively mild effect on orangutan distribution patterns. The current range of the orangutan will most likely not contract considerably, with a reduction of between 3 and 7% predicted by three out of four climate models. The exception is the CSIRO model, which predicts a much larger range reduction under both scenarios (around 15% under A2a and 13% under B2a). This appears to be the result of an increase in feeding time caused by changes in precipitation patterns; the CSIRO models predict the largest increases in mean annual rainfall under each scenario. However, rainfall increases more in the NIES99 model under the A2a scenario than the CSIRO model under the B2a scenario, yet the range reduction is considerably less (only 6.61%). The dramatic range reduction under the CSIRO models is therefore likely to be the result of regional increases in rainfall specifically within the orangutan range. Changing precipitation patterns could have both a direct effect on feeding time allocations and an indirect effect through their influence on diet. As there is considerable uncertainty in climate predictions, the results predicted under the CSIRO model should be treated with caution; however, they do highlight the vulnerability of the orangutan to changes in feeding time, caused by changing precipitation patterns.

The models did not produce a consistent effect of climate change on group sizes within the areas where the orangutan is predicted to persist. Although under the CSIRO models group sizes were projected to decrease, the other models predicted either an increase in group size or no significant change. Group size in orangutans therefore appears to be sensitive to variations in climate predictions, but if indeed a group size of close to one individual is a viable minimum, orangutans appear to be somewhat buffered against the effects of climate change.

However, the changes in climate conditions are likely to force orangutans to shift some of their behavioural patterns. Although resting time demands may go down (with 6 out of 8 model/emissions scenario combinations predicting a decrease), moving time demands may become increasingly high (with 5 out of 8 model/emissions scenario combinations predicting an increase). Feeding time appears less likely to change in the future, with only 2 model/emissions scenario combinations predicting an increase in feeding time allocations. However, higher moving time demands will in turn lead to increased energy requirements, which will have a knock-on effect on other time budget variables. Feedback loops like this are not currently included in the model, but it is important to consider them as they may lead to exaggerated effects of climate change on orangutan populations.

It is important to note that the models may be seriously underestimating the effect of climate change on the orangutan. The possible effects of climate change on the energy content of orangutan food sources and on the percentage of forest cover were not incorporated into the model. Although the response of tropical forests to climate change is extremely uncertain (Clark, 2004), it is possible that the increased temperatures could lead to considerable forest dieback and an increase in the frequency and severity of forest fires (Allen et al., 2009; Bonan, 2008). The percentage of forest cover was found to be an important variable in the time budget model; therefore if climatic change causes strong negative effects on forest cover, this could be devastating for the remaining orangutan populations. Furthermore, the effect of future deforestation was not incorporated in the model. Future research is needed to investigate the inclusion of both the effect of climate change on forest cover as well as deforestation projections to provide more realistic predictions of the future distribution of the orangutan. Finally, the statistical downscaling procedure used to generate these data at a high resolution may lead to uncertainties in climate estimations (Ramirez & Jarvis, 2010).

Although the orangutan time budget model suggests that the effect of climate change and human population growth on the orangutan will be relatively small, commercial logging and the conversion of forests for plantations continues unabated in Borneo and Sumatra (Koh et al., 2011; Miettinen et al., 2011a), rapidly destroying and fragmenting the remaining orangutan habitat. Forest fires consume vast tracts of rainforest as well as the orangutans that inhabit them, while hunting for both bushmeat and for the pet trade reduce populations to critically low levels (Nellemann et al., 2007). Thus, orangutans are currently extremely vulnerable to extinction and even a small decline in their range due to climate change may have a large impact on the survival chances of the species.

5. Conclusion

Although the predicted effect of climate change on orangutan biogeographical ranges appears to be relatively mild, it is important to remember that there are other more imminent threats to orangutan survival. In addition, the results of this study highlight the precarious balance between climate, behaviour and biogeography – if one of the components is affected this can have knock-on effects on other variables, exaggerating the consequences for orangutan populations. Moving and feeding time demands, for example, are predicted to become more severe in the future, while resting time may become less restrictive, and these changes will have secondary effects on other variables. It is worrying that orangutans were predicted to lose up to 15% of their habitat under one of the climate change scenarios, especially considering that the effects of land and forest cover changes were not incorporated in the climate change models. However, it is important to mention that future climate predictions remain tentative, and the regression equations did not produce a perfect fit to the data leading to further uncertainty in model predictions. Overall, the results indicate that the current range of the orangutan will decline by approximately 3-7% by 2080 as a direct result of climatic change and human population growth, although this is likely to be an underestimate as land and forest cover changes were not included. However, even a range reduction of 5% may have a dramatic effect on the survival of the two orangutan species, particularly as suitable habitat becomes more fragmented through deforestation.

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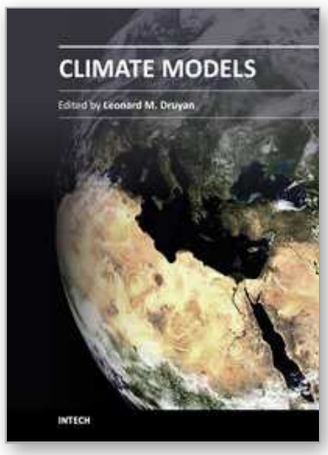
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