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Fission–fusion social systems as a strategy for coping with ecological constraints: a primate case

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Abstract Fission–fusion social systems, in which members of a social community form frequently changing subgroups, occur in a number of mammalian taxa. Such systems are assumed to be a response to the costs of grouping, but evidence to support this hypothesis is limited. We use a linear programming approach to build a time budget model that predicts the upper bound on group size in order to test the hypothesis that fission–fusion social systems are the outcome of time constraints. Comparative data from 14 wild chimpanzee (*Pan* spp.) populations are used to derive a set of equations defining the relationship between climatic variables and time budget components, which are then used to calculate the upper limits on group size that can be maintained in different habitats. We validate the model by showing that it correctly predicts the presence/absence of chimpanzees across sub-Saharan Africa and the group sizes observed in natural populations. The model suggests that the costs of travel are limiting for chimpanzees. Chimpanzees can reduce these costs dramatically by fissioning their bonded communities into small foraging parties. If they did not, they would be unable to live in any habitats where they currently occur.

Keywords Time budget model · Chimpanzees · Fission–fusion · Biogeography · Group size

Introduction

For social animals, living in a group not only brings benefits but also incurs costs (Alexander 1974) and a species' social organization as well as its group size is usually

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seen as the result of an optimization process, which maximizes benefits while minimizing costs. However, costs and benefits of group living are specific to the habitat, and observed social structures should not be understood as a species-specific trait *per se* but rather as a trade-off of species-specific requirements in a given habitat. The complexity of the interaction between ecological variables and social organization/group size is further enhanced by the fact that many social species have evolved behavioural strategies to reduce the costs of group living. For example, one way to overcome intense competition in large groups is by temporarily dispersing into smaller groups (Kummer 1971; Van Schaik and Van Hooft 1983). Although many group-living animals will occasionally split into smaller groups over the course of the day, some species do this on a very regular basis. Such species are said to have fission–fusion societies, and include hyenas (Owens and Owens 1978), bottlenose dolphins (Smolker et al. 1992), spider monkeys (Klein and Klein 1997/1977), chimpanzees (e.g. Nishida 1968) and humans (Rodseth et al. 1991).

Chimpanzees represent the classic case of a fission–fusion society. Although they live in a tightly bonded group ('community') in which all members know each other individually and defend a communal home range, they regularly split into smaller groups ('parties'), which change frequently in size and composition (about every 14–126 min; see Boesch and Boesch-Achermann 2000). The community as a whole is rarely seen together at one place (Goodall 1986). We do not yet understand why such a system has evolved but several studies have linked fission–fusion parameters to a variety of ecological variables, suggesting that fission–fusion serves to overcome intra-group competition. Chimpanzee party size has been linked to predation pressure (Boesch 1991; Sakura 1994), number of receptive females in a party (e.g. Goodall 1986; Mitani et al. 2002a), food availability (e.g. Anderson et al. 2002; Chapman et al. 1994; Itani and Suzuki 1967; Wrangham 1986b) and demographic factors (Goodall 1986; Lehmann and Boesch 2004; Newton-Fisher 1999a; Newton-Fisher et al. 2000). However, surprisingly few studies have investigated the actual costs and benefits of such a fluid system in any depth and the relationship between party size, community size and ecological variables remains unclear. Furthermore, what has never been explored in any detail is the role of time as an ecological constraint in fission–fusion species.

In this study we use a modelling approach to investigate the evolutionary ecology of fission–fusion social systems by asking how the formation of small subgroups in chimpanzees (*Pan troglodytes* and *Pan paniscus*) affects individual time budgets. Specifically, we ask whether the fluid structure of their social system enables chimpanzees to live in habitats in which they could otherwise not survive. Our approach consists of four steps: firstly we determine the ecological and demographic factors affecting chimpanzee time budget. Secondly we use these relationships to build a taxon-specific time budget model, which allows us to predict maximum ecologically tolerable group sizes for chimpanzees across Africa. We then validate this model against known distribution data. Finally, we use this model to 'experimentally' assess the importance of subgroup formation for chimpanzee distribution and group sizes.

Our model uses individual time budgets and is based on the linear programming approach developed by Dunbar (1992c, 1996). Time budget models of this kind are based on the assumption that an animal's behaviour is ultimately limited by the fact that it only has a set amount of time available each day in which to meet its essential activity demands (in the form of feeding, moving and social interaction) (Dunbar 1992b, c, 1996). The demands for the various components of a time budget are

determined by the way the species' physiology interacts with the specific characteristics of a particular habitat, as well as by aspects of demography such as group size (Caraco 1979). The model then aims to predict the amount of time a virtual animal ought to devote to each of the time budget components under a given set of climatic and demographic conditions. If several animals can meet their individual requirements when living together in a group, the species could in principle occur in that specific habitat (Dunbar 1996).

Thus, once we know the relationships between group size, climate variables and time budget components for chimpanzees, we can use them to calculate the maximum ecologically tolerable group size at which individual chimpanzees can still meet the habitat-determined demands on their time budget without exceeding the gross amount of time available during the day. In the model, feeding, moving and grooming time are assumed to be determined by some combination of climatic and demographic variables; in contrast, resting time is viewed as a source of 'uncommitted time' that can be converted into more urgent activities when required, although there may be a minimum allocation of time that animals have to spend resting due to climatic or other factors (Dunbar and Dunbar 1988; Dunbar and Sharman 1984). These models are designed to predict the maximum group sizes that a species can maintain in a given habitat. However, other variables, such as predation pressure and the occurrence of infanticide, may add additional constraints to the species' survival: a certain minimum group size may be required to allow an individual to cope with some other critical ecological constraints (e.g. minimizing predation risk) (Dunbar 1996).

The aims of our study are twofold. First, we aim at investigating the interrelation between climate, group size and time budget components, so as to identify possible causal links between ecological factors and chimpanzee distribution. Second, we investigate how chimpanzees benefit from a fission–fusion social system, i.e. what evolutionary path may have led to such a social system. Our model should indicate which advantages fission–fusion has versus a more coherent social structure and how this affects chimpanzee group sizes and biogeography. Thus our modelling approach will provide insight into the effectiveness with which a fission–fusion social system allows animals to minimize the costs of group-living. It will also give insights into how behavioural/social flexibility at the level of the group can translate into biogeographic scales.

Materials and methods

The data

We scanned the literature for studies, which gave quantitative data on chimpanzee community sizes and structure (e.g. community size, party size, demography), time budgets (e.g. percentage of time spend feeding, resting, travelling and socialising), diet (e.g. percentage of fruits and leaves in the diet, number of food species) and ranging patterns (e.g. daily travel distance, home range size). In total, data from 30 different study sites were collated. If data from several years/studies were available for one population, we used those years for which we had the most complete time budget and demographic data. In those cases where there were either no time budget data or where time budgets were available for several years, we averaged the

Table 1 Summary (and references) of demographic and behavioural data used for model equations

Site ID	Country	Park	Species	Hab	Prov	Com _{size}	AF	AM	Party _{size}	% Fruit	% Leaf	% Feed	% Rest	% Move	% Groom
CL_Tai ^a	C. d'Ivoire	Tai	<i>P.t. verus</i>	Yes	No	72	25	7	5.8	76	18	52.5	(16)	17	
DC_Kb ^b	DR Congo	Kahuzi-Biega	<i>P.t. schweinfurthii</i>	Semi	No	22	3	5	4.5	38					
DC_Lom ^c	DR Congo	Lomako	<i>P. paniscus</i>	Semi	No	[28]			6.7	72	25	40.4	32	16.1	5.7
DC_Wam ^d	DR Congo	Wamba	<i>P. paniscus</i>	Yes	Yes	65			16.9	83	15	30	(29.6)	13	
EG_Oko ^e	Equ Guinea	Okoro Biko	<i>P.t. troglodytes</i>	No	No	[42]			11.2			40.8	(22)	27.6	
Ga_Lop ^f	Gabon	Lope	<i>P.t. troglodytes</i>	No	No				2.4	69	19				
Gu_Bos ^g	Guinea	Bossou	<i>P.t. verus</i>	Yes	No	19	7	2	5	57	14	34.6	44.7	9.9	10.8
Se_Fon ^h	Senegal	Fongoli	<i>P.t. verus</i>	Semi	No	27				66	17				
Se_Mas ⁱ	Senegal	Mt Assirik	<i>P.t. verus</i>	No	No	28	5	6	4.7	57	10	44	15	36	5
Ta_Gom ^j	Tanzania	Gombe	<i>P.t. schweinfurthii</i>	Yes	No	52	19	6	5.2	51	25	47	33.8	13	6.2
Ta_Mah ^k	Tanzania	Mahale	<i>P.t. schweinfurthii</i>	Yes	Yes	[90]	36	10	8.6	48	22	30.3	36.3	20.5	12.9
Ug_Bud ^l	Uganda	Budongo	<i>P.t. schweinfurthii</i>	Yes	No	56	12	13	6.4	75	18	52.8	25	7.5	14.3
Ug_Kib ^m	Uganda	Kibale	<i>P.t. schweinfurthii</i>	Yes	No	[120]	40	25	5	80	14	57.3	20.9	11	10.8
Ug_Sem ⁿ	Uganda	Semliki	<i>P.t. schweinfurthii</i>	Semi	No	45			4.8	39	30				

In some cases where data from more than one study were available we used averages; data in () indicate calculated values (see text for details), while data in [] indicate estimations (based on published data) when no data were available for the year when time budget data were collected; time budgets and party sizes from Wamba and Mahale were excluded from the equation-finding process because chimpanzees were provisioned when the data were collected

Hab = habituation, Prov = provisioning, AF = adult females, AM = adult males, Com_{size} = community size, P.t. = *Pan troglodytes*

^aBoesch and Boesch-Achermann (2000), Doran (1997) and Lehmann and Boesch (2003, 2004)

^bYamagiwa et al. (1996)

^cBoesch and Boesch-Achermann (2000) and White (1992, 1996)

^dKano and Muiawwa (1984)

^eJones and Sabater Pi (1971)

^fTutin and Fernandez (1993) and Tutin et al. (1997)

^gSakura (1994), Sugiyama and Koman (1987), Takemoto (2004) and Yamakoshi (1998, 2004)

^hJ. Pruez (personal communication)

ⁱMcGrew et al. (1988) and Tutin et al. (1983)

^jGoodall (1968, 1983, 1986), Wrangham (1975, 1977) and Wrangham and Smuts (1980)

^kMatsumoto-Oda (2002), Nishida (1990), Nishida et al. (2003) and Nishida and Uehara (1983)

^lFawcett (2000), Newton-Fisher (1999b), Reynolds and Reynolds (1965) and Tweheyo et al. (2004)

^mGhiglieri (1984), Mitani et al. (2002a), Watts (2000) and Wrangham (1986a)

ⁿHunt and McGrew (2002)

available data over years, so that only one datum per study site was used to ensure statistical independence. The behavioural data from 14 study sites used for finding the time budget equations are summarized in Table 1.

Climate data for the chimpanzee study sites were primarily derived from original long-term studies at the sites as provided in the literature. For those study sites, for which we did not find original climate data, we used data from the Willmott and Matsuura (2001) weather database. Willmott and Matsuura (2001) provide a global dataset of monthly and annual temperature and rainfall in grids of 0.5° latitude by longitude, based on a combination of the Global Historical Climatology Network (version 2) and Legate and Willmott's (1990a, b) weather station records of monthly and annual mean air temperature and total precipitation. For each site for which climate data were required, we calculated average values over those data points in the Willmott and Matsuura dataset that fell within a radius of 0.5° longitude and latitude to the site. We also used the data from Willmott and Matsuura to compile a dataset containing climate details for Africa on a 0.5° longitude and latitude grid. This dataset consists of 11,670 data points (and does not include sites used for deriving time budget equations) and is used to test how accurately our time budget models can predict chimpanzee distribution across Africa.

The following climate variables were used in this study: mean annual rainfall in mm (P_{ann}), mean annual mean temperature in $^\circ\text{C}$ (T_{ann}), temperature variation between months (calculated as the standard deviation across average values for 12 months: T_{moSD}), average rainfall per month in mm (P_{mo}), rainfall variation between months (measured as the standard deviation across average values for 12 months: P_{moSD}), number of months per year with <50 mm of rainfall ($P < 50$), number of months per year with <100 mm of rainfall ($P < 100$) and the plant productivity index P2T [the number of months in the year in which rainfall (in mm) was more than twice the average monthly temperature (Le Houérou 1984)]. P2T is used as a measure of the growing season in tropical habitats, as it yields a very strong correlation with primary productivity (Le Houérou 1984), while $P < 50$ and $P < 100$ can be regarded as alternative measures of seasonality. Previous models of primate socio-ecology have shown that these variables can be important determinants of time budget (Dunbar 1992b, c; Hill and Dunbar 2002; Korstjens et al. 2006; Korstjens and Dunbar 2007; Williamson and Dunbar 1999). In addition, we also used AVHRR satellite data on forest cover from DeFries et al. (2000) to determine the percentage of forest cover for each of our sites. Climatic data for the chimpanzee study sites are summarized in Table 2.

The model: equation-finding process

The first step in building the model is to find the set of multivariate equations that account for the highest proportion of variance in the core time budget components. We used multiple regression and curve estimation procedures to determine the factors that influence the percentage of time that chimpanzees invest in each component of the time budget. Basic biological considerations were used to decide which variables should be included as potential independent variables at each stage (see Dunbar 1992a). Sites at which chimpanzees were provisioned around the time when time budget data were collected (Wamba and Mahale) were excluded from the dataset as provisioning is likely to alter time budget components as well as party sizes in chimpanzees (Wrangham 1974).

Table 2 Summary of climate data used to derive the model equations

Site ID	Lat	Lon	Alt	P_{ann}	T_{ann}	P_{mo}	$P_{mo}SD$	$T_{mo}SD$	P2T	$P < 50$	$P < 100$
CI_Tai	5.87	-7.33	90	1,781	25.5	148.0	87.66	0.88	9.6	2.4	4.4
DC_Kb	-2.08	28.75	2,200	1,586	20.1	137.8	59.98	0.38	12	1.5	3.0
DC_Lom	0.83	21.08	390	1,935	24.8	161.3	50.70	0.53	12	0.0	2.0
DC_Wam	0.03	22.58	400	2,002	25.0	170.3	42.74	0.24	12	0.0	0.3
EG_Oko	1.47	9.87	750	2,112	21.0	201.5	119.10	1.17	11.7	0.5	2.8
Ga_Lop	-0.17	11.58	425	1,531	25.5	140.4	98.67	1.09	9.0	3.0	3.8
Gu_Bos	7.39	-8.3	550	2,195	23.6	182.9	137.80	1.42	9.0	3.5	4.0
Se_Fon	12.65	-12.22	50	1,334	28.2	110.4	136.38	2.47	5.5	6.5	7.0
Se_Mas	12.88	-12.77	206	955	29.0	79.6	90.95	2.45	5.7	6.0	7.3
Ta_Gom	-4.67	29.63	1,092	1,820	24.5	118.1	100.70	0.62	8.0	4.0	5.5
Ta_Mah	-6.12	29.92	1,618	1,699	24.3	146.7	119.53	1.49	7.7	4.0	5.0
Ug_Bud	1.73	31.55	1,100	1,679	21.0	139.9	61.93	0.75	10.2	1.8	4.5
Ug_Kib	0.45	30.42	1,500	1,702	19.8	141.2	74.55	0.44	10.2	2.1	4.4
Ug_Sem	1.25	30.47	1,100	1,200	27.0	94.9	45.95	0.66	11.0	1.0	5.0

Data were derived primarily from published studies. Only if those were not available or measured over a short period of time we used data from the Willmott and Matsuura database (adapted from Willmott and Matsuura 2001)

Lat = latitude, *Lon* = longitude, *Alt* = altitude, P_{ann} = mean annual precipitation, T_{ann} = mean annual temperature, P_{mo} = mean monthly precipitation, $P_{mo}SD$ = mean monthly variation in precipitation, $T_{mo}SD$ = mean monthly variation in temperature, *P2T* = mean number of months in a year in which rainfall is higher than twice the average monthly temperature, $P < 50$ = mean number of month with <50 mm of precipitation, $P < 100$ = mean number of month with <100 mm of precipitation

Feeding and moving

Feeding and moving time were assumed to be independently determined by climate, diet, party size and/or community size.

Social time

Social time is assumed to be an important factor for group cohesion (and hence their resistance to fission). It is important to differentiate the amount of time that ought to be devoted to grooming in order to prevent groups from breaking up from the actual amount of time spent grooming at a particular site by animals living in a community of a particular size (which may be less because grooming time might be temporarily traded for more urgent activities; see, for example, Altmann 1980; Dunbar and Dunbar 1988) at the cost of group cohesion. In order to determine the former, we have used a generic grooming equation obtained from a re-analysis of an updated version of the Dunbar (1991) dataset on Old World Monkeys and Apes (Dunbar 1991, 1992a). This re-analysis is based on the relationship between mean group size and mean time spent engaged in grooming activities for a sample of 39 African primate species and incorporates various life history variables as well as phylogenetic effects (Lehmann et al., *in press*). With this approach, the amount of time that ought to be spent on grooming or social activities in order to keep the community together was estimated using the equation:

$$\text{Groom (\%)} = 1.55 + 0.23 \times \text{community size.}$$

In effect, this equation defines the amount of time that is needed to maintain the social coherence of a community of a particular size through time.

Resting

The model assumes that resting time is made up of two independent components: enforced resting time (which is probably climatically driven) and uncommitted resting time that is not otherwise required for feeding, moving or social activities. In order to know how much uncommitted resting time animals have available to convert into the other core activity categories, we need to know the minimum value of enforced resting time. Enforced resting time is most likely to be a consequence of the fact that animals are unable to engage in energetically costly activities when ambient temperatures rise above a critical threshold, and are thus forced to rest. Unfortunately, the values for resting time given in the chimpanzee literature do not allow us to distinguish between the two components of resting time. However, we can circumvent this problem if we recognize that, unless chimpanzees always live at their maximum possible community size, observed resting time will invariably be higher than the enforced resting time under any given climatic condition. We use this fact to derive an expression for enforced resting as a function of community size and environmental variables (for details, see Sect. 'Results'). One further problem is that some authors include social time in resting time, so that resting time needs to be corrected in these cases. We have done this by calculating the expected social time using the above equation for social time and subtracting this value from that given for resting time in those cases where social and resting time were combined.

Party size

Average party size is assumed to be primarily driven by ecological conditions (Boesch 1996; Chapman et al. 1995; Matsumoto-Oda et al. 1998; Wrangham 1977, 2000; Wrangham et al. 1992), such as food distribution and predation pressure. Since no quantitative data for predation pressure are available, average party size estimations were based only on climatic variables.

The model: output variables

The model uses the equations for the above variables to calculate for each of the sites in our database the maximum ecologically tolerable community size, following the procedure described in Dunbar (1992c). The model uses a starting community size of one individual and calculates that individual's time budget. If the sum of the time budget variables does not exceed 100%, community size is then increased algorithmically by one individual at a time until the sum of all time budget variables exceeds 100%; the maximum ecologically tolerable community size is then defined as the community size of the previous cycle. In order to avoid anomalous outcomes, all time budget equations were constrained to have minimum values of 5% and maximum values of 99%. Party size was not allowed to exceed community size and was constrained to a minimum of two individuals (e.g. mother and offspring) when community size was larger than 2. Chimpanzees were considered able to live at a particular site if (1) predicted maximum ecologically tolerable community size was

larger than 10 (almost all known chimpanzee populations live in larger communities) and (2) when forest cover of this site was more than 20%. Minimum required forest cover for chimpanzees was set to 20% because this approximates the minimum value of forest cover of the sites at which chimpanzees are known to occur (21%).

The model: validation and test

The model was validated in several ways. First, we tested how accurately the model predicts the presence and absence of chimpanzees in forested National Parks across sub-Saharan Africa for which we know whether or not chimpanzees are present. Second, we test how accurately the model predicts community size at the sites where community size is known. Finally, the Willmott and Matsuura dataset was used to test how well our model predicts the general distribution of chimpanzee across the whole of Africa.

Data on presence and absence of chimpanzees across Africa were obtained by screening the primate literature and the Internet, especially the UNEP and WCMC World database (www.unep.com) on protected areas and from GRASP (Butynski 2001; Caldecott and Miles 2005; Kormos et al. 2003). To preserve statistical independence, only sites separated from each other by at least 1° of longitude and latitude were included. Our dataset consists of 309 independent sites across Africa, 150 of which reported the presence of chimpanzees. This data set includes the sites from Table 1 to allow us to compare predicted and observed values for group size.

The effects of fission–fusion

To evaluate the effects of subgroup formation on chimpanzee biogeography and community size, we re-ran the model setting party size equal to community size on each cycle. This simulated the effect of the chimpanzees remaining in a single cohesive group.

Statistics

Data on chimpanzee behaviour were tested for normality using skewness and kurtosis values. For screening the data and the relations between ecological and time budget variables, we used scatter plots (to find possible curvilinear relations) as well as bivariate Pearson correlation analyses. Linear regression and curvilinear estimation procedures (such as quadratic or logarithmic functions) were then used to obtain multivariate equations for each dependent variable of interest. Finally, we used a linear program in Dbase to calculate maximum ecologically tolerable community size for each location in the dataset. The predictive power of the model was calculated by comparing the number of correct and incorrect classification by the model to a random distribution using log-likelihood goodness of fit statistics. We used Mann–Whitney *U* tests (MWU) to compare predicted time budget components and community/party sizes between correctly and incorrectly classified sites, and one-sided Wilcoxon Signed Ranks tests (WSR) to compare predicted and observed values. One-sided statistics are justified in this case as we test the model's explicit prediction that predicted community sizes will necessarily be larger than observed values. All analyses were done using SPSS 12.0.1 for Windows.

Table 3 Equations used in the model

	Equation	Adj. R^2	F	n	P
Feeding	$30.958 + 1.035 \times P < 100 + 0.205 \times Com_{size}$	0.76	12	8	0.012
Moving	$102.144 - 0.11 \times P_{ann} + 2.859125598 \times 10^{-5} \times P_{ann}^2 + 2.587 \times Party_{size}$	0.76	8.4	8	0.03
Rest	$17 - 1.477 \times latitude$	0.77	12.4	8	0.01
Party _{size}	$21.489 + 0.072 \times frcover - 0.33 \times P_{mo} + 0.0012 \times P_{mo}^2$	0.52	4.87	12	0.014
Grooming	$1.55 + 0.23 \times Com_{size}$	Generic equation for OWM and apes			

$P < 100$ = mean number of month with <100 mm of precipitation, Com_{size} = community size, P_{ann} = mean annual precipitation, $frcover$ = forest cover, P_{mo} = mean monthly precipitation

Results

The equations

All data on chimpanzee behaviour were normally distributed (all skewness values within twice their standard errors). The best-fit equations generated by the equation-finding process are summarized in Table 3. Feeding time was predicted by community size and the number of months with rainfall <100 mm, indicating that feeding time is higher in larger communities as well as in more seasonal areas. Moving time was best predicted by party size and annual rainfall. Larger parties spend more time moving. The relation with rainfall follows a U-shaped function with highest moving times in either very dry or very wet habitats. Both types of habitat presumably produce very clumped food sources, so that individuals have to move relatively long distances between food patches. Resting time was highly influenced by community size (i.e. chimpanzees rested less when in larger communities), supporting our hypothesis that a large part of resting time is based on uncommitted time not used for other activities. The relationship between resting time and community size followed an inverse function, with an additional linear effect of latitude:

$$\%resting = 13.019 + 1.634 \times (428/\text{community size}) - 1.477 \times latitude$$

($R^2_{adj} = 0.77$, $F = 12.4$, $n = 8$, $P = 0.01$). Because the model only requires the enforced resting component, which is independent of community size, the community size at which the inverse function for resting time began to reach its asymptotic value was estimated. This value was then used to calculate the new intercept for the effect of latitude on resting, thereby yielding the equation for minimum required resting time given in Table 3. Finally, party size was best predicted by a quadratic relationship with monthly rainfall and by forest cover. Parties are larger in very dry and very wet habitats (probably due to relatively clumped and dispersed food patches in such habitats) and in more dense forests. Interestingly, none of the dietary variables, the percentage of fruits or leaves in the diet or the number of food species available explained any of the variation in time budget variables or party size.

The model

The equations given in Table 3 were then used in a simulation model to determine the maximum ecologically tolerable community size for habitats representing

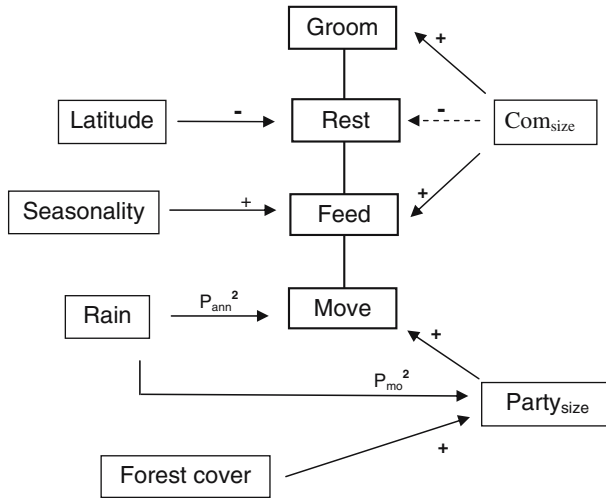


Fig. 1 Flow chart depicting the relations between climatic, demographic and behavioural variables based on the equations in Table 1. Plus symbol, minus symbol and 2 , indicate whether the effect is positive, negative or quadratic; arrowheads indicate assumed causal directions. $P < 100$ = mean number of months with <100 mm of precipitation; Com_{size} = community size; P_{ann}/P_{mo} = mean annual/monthly precipitation

different combinations of climatic variables. Figure 1 depicts the flow chart specifying the relationships between the various variables involved. The most important climatic variables are rainfall and rainfall seasonality, while temperature-related variables do not affect chimpanzee time budgets.

Predictive power

The model was first run using the climatic data for the sites in our African database. Table 4 shows the distribution of correct and false predictions for chimpanzee presence/absence at all the sites in our database. The model correctly predicts the presence and absence of chimpanzees in 78% of all cases, which is significantly better than expected by chance ($G = 236.4$, $n = 309$, $df = 1$, $P < 0.0001$). The majority of wrongly classified locations are within the known geographical distribution of chimpanzees, in many cases close to where chimpanzees are known to

Table 4 Number and percentage of sites correctly and incorrectly classified by our model

	Observed	
	Absent	Present
Predicted Absent	92	2
Predicted Present	67	148
% correct	58%	99%

The low value for the prediction of chimpanzee absence is primarily due to the fact that our model fails to predict the patchy present day distribution of chimpanzees but predicts chimpanzee to be present throughout their geographical range (see also Fig. 2)

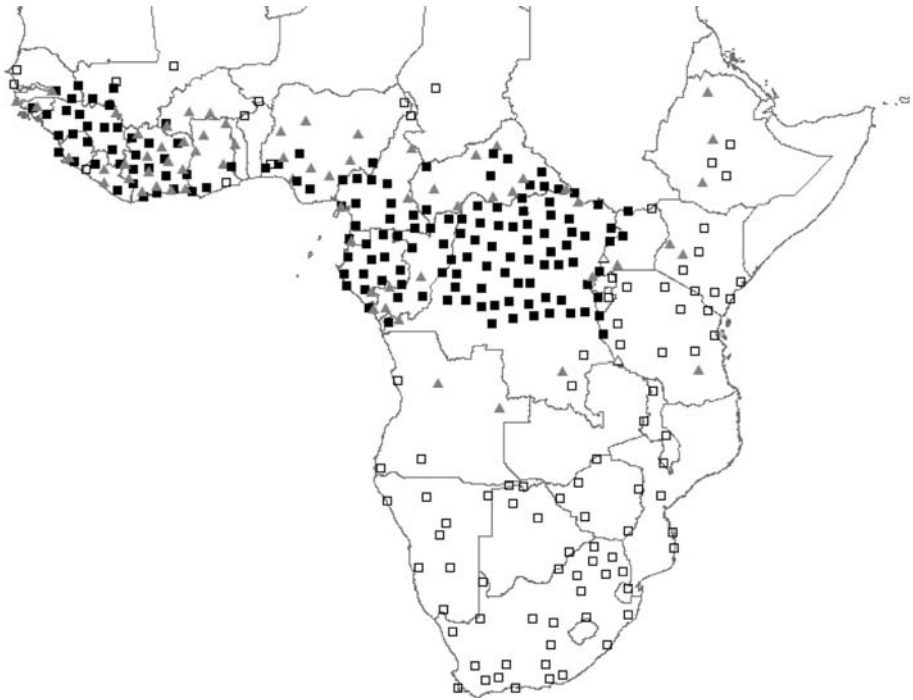


Fig. 2 Observed and predicted presence and absence of chimpanzees for selected forested National Park sites across Africa. *Open square* indicate sites for which the absence of chimpanzees was correctly predicted, *filled square* indicate sites for which presence was correctly predicted, *filled upward triangle* indicate sites for which presence was falsely predicted and *open upward triangle* indicate sites for which absence was falsely predicted

occur: the model predicts that chimpanzees could occur at these sites, even though no chimpanzees have been observed there within the past century or so (i.e. since reliable records have been available) (see Fig. 2).

Community size and party size

Mean (\pm SD) predicted community size at sites where chimpanzees were correctly predicted to be present is 77 ± 22.6 individuals. These values are within a realistic range for chimpanzees, but since the model is designed to predict maximum ecologically tolerable community sizes, predicted community sizes are expected to exceed the observed values of 51 ± 28 individuals for community size. Predicted values for party size average 5.6 ± 2.1 , while observed values average at 6.7 ± 3.4 individuals ($n = 14$). Figure 3 compares the predicted values for community size with those actually observed at specific sites, using sites where chimpanzees were correctly classified as present. Recall that the models are designed to predict the *maximum* ecologically tolerable community size: observed community sizes should thus lie below the main diagonal of the graph (the line that demarcates points where observed and predicted values are the same). Predicted community sizes are significantly larger than observed values (WSR: $n = 11$, $z = -2.4$, $P = 0.02$). Note that in the two cases where observed values exceed predicted values, the values in fact lie

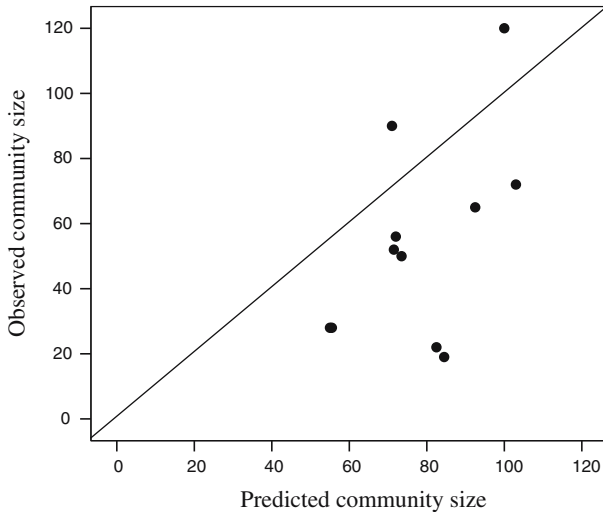


Fig. 3 Observed and predicted community sizes; the *line* demarcates equal values. Note that the model predicts maximum ecologically tolerable community sizes and values should therefore lie below the *diagonal*

very close to the main diagonal. Comparing sites at which chimpanzees were correctly predicted to be present with those where they were falsely predicted to be present (false positives) shows that although there was no significant difference in predicted community size (median_{cor} = 82.75, inter-quartile range 67.6–90.5; median_{false} = 72, inter-quartile range 50.5–94; MWU: $n = 215$, $z = -1.8$, $P = 0.08$), party sizes were significantly smaller at false positive sites (median_{cor} = 5.2, inter-quartile range 5–5.9; median_{false} = 5, inter-quartile range 4–5.6; MWU: $n = 215$, $z = -2.6$, $P = 0.01$).

Chimpanzee biogeography

To determine how time budget variables influence chimpanzee distribution across Africa, we compared the time budget components of those sites where the model correctly predicted chimpanzees to be absent to those where the model correctly predicted chimpanzees to be present. We found that, at sites where chimpanzees were absent, predicted resting, moving and feeding times were all significantly higher than at sites where chimpanzees were correctly categorized as present (MWU_{feed}— $z = -11.1$, $n = 240$, $P < 0.0001$; MWU_{rest}— $z = -8.5$, $n = 240$, $P < 0.0001$; MWU_{move}— $z = -12$, $n = 240$, $P < 0.0001$).

Predicting chimpanzee distribution across Africa

As a final validation of the model, we used our large African climate dataset based on Willmott and Matsuura (2001) to predict the distribution of chimpanzees. As can be seen in Fig. 4, the model provides a good fit to the known chimpanzee distribution, but overestimates the extent of their distribution into the south (e.g. Angola). Although our model identifies these more southerly habitats as being suitable for chimpanzees, chimpanzees are not known ever to have existed in these

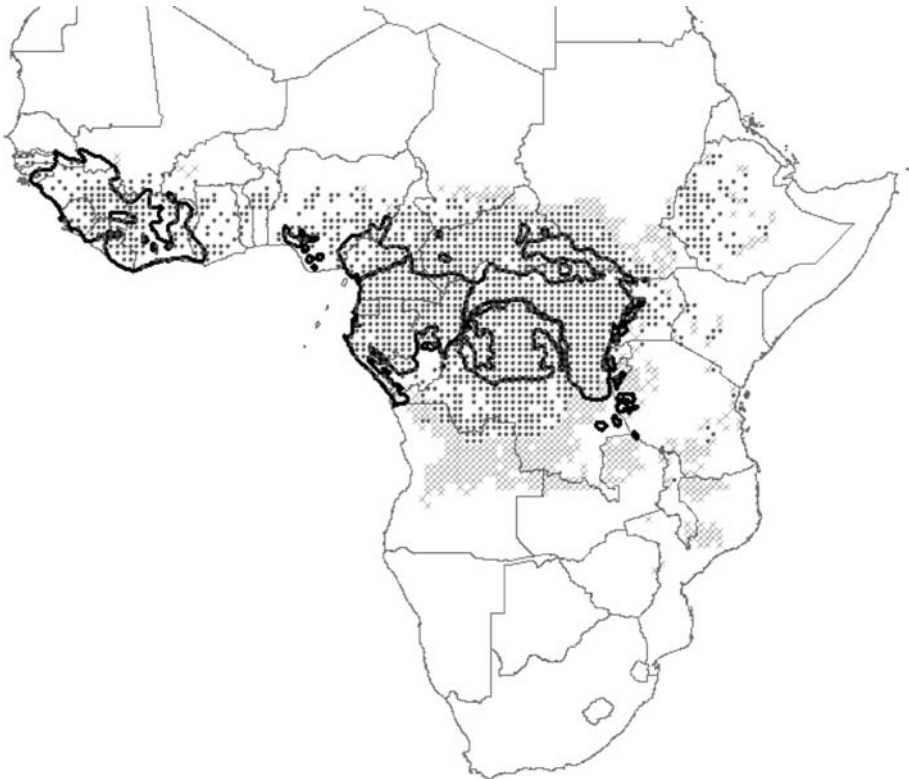


Fig. 4 Distribution of *Pan* as predicted by the time budget model (with and without allowing for fission–fusion), using a lattice of quadrats evenly covering sub-Saharan Africa based on the Willmott and Matsuura climate database. *Dark circles* indicate sites for which the presence of chimpanzees was predicted irrespective of fission–fusion. *Grey circles* indicate locations for which the presence of chimpanzees was predicted only when the model allowed for fission–fusion. *Blank quadrats* are those in which predicted group size is below the minimum set value of 10. The present day known range of *Pan* distribution is indicated by the *black polygons* (following GRASP)

regions. Apart from the possibility of geographical barriers limiting the southern distribution of chimpanzees (notably the Congo River and the presence of an intervening savannah belt), one explanation for the overestimation may be that the minimum viable community size in these locations may exceed the maximum ecologically tolerable size. For the range of habitats available in sub-Saharan Africa, predicted maximum ecologically tolerable community sizes are bi-modally distributed, with a distinct trough at community sizes of about 45 individuals (Fig. 5). Interestingly, communities with fewer than 45 individuals are found exclusively at the periphery of the predicted distribution. In fact, all communities for which maximum ecologically tolerable community sizes were predicted to be below 45 occur in areas where chimpanzees are not present, while predicted maximum ecologically tolerable community sizes within the biogeographical range of chimpanzees are considerably larger (see Fig. 5). Note, however, that this threshold value relates to maximum ecologically tolerable community sizes and does not set a value for minimum viable community size in observed chimpanzee populations. Observed values may well be below the threshold value (see Table 2), but our model suggests

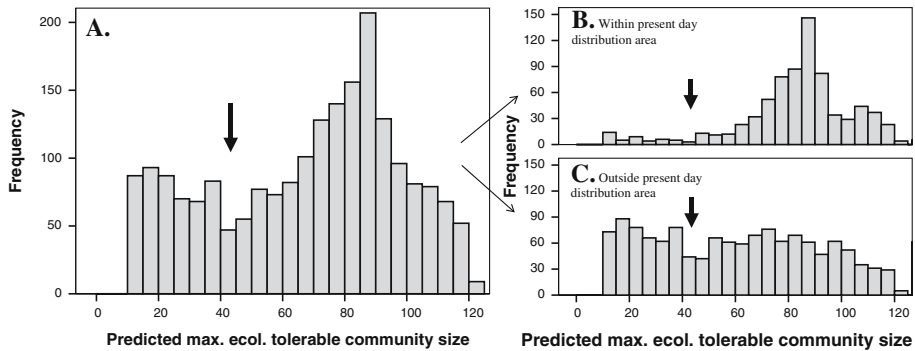


Fig. 5 Histogram (A) of predicted maximum ecologically tolerable community sizes for sites that were classified by the model as suitable for chimpanzees. The two smaller histograms depict the same data for locations within (B) and outside (C) the known present day distribution of *Pan*. The block arrows indicate the minimum between the two modes in (A), which we identify as a likely minimum value of maximum ecologically tolerable group sizes for viable chimpanzee communities, as almost all values for locations within the biogeographical range of chimpanzees are above this value

that habitats in which maximum ecological community sizes cannot exceed 45 individuals may not be able to sustain viable chimpanzee populations. Possible reasons for this may be that chimpanzees in these more marginal habitats are likely to experience higher inter-group competitions and/or are subject to higher levels of predation risk, both of which may require larger groups.

The effects of fission–fusion

The model presented above incorporates the effects of fission–fusion on chimpanzee ecology. In this final step, we use the model to ask what advantages fission–fusion provides for chimpanzee time budgets. In order to do this, we re-ran the model setting party size equal to community size on each cycle (i.e. preventing chimpanzees from subgrouping). Using the Willmott and Matsuura database, the predicted chimpanzee distribution when the community always stays together as a coherent group (i.e. party size equals community size in the model) is about 14% smaller than the predicted distribution with fission–fusion, although the model still predicts chimpanzees to be present throughout their actual range (see Fig. 4). However, as can be seen in Fig. 6, maximum ecologically tolerable community size has decreased from a median value of 74 to 16 individuals (with almost no variance around this value) and is thus much smaller than any known chimpanzee community. In fact, if we assume that maximum ecologically tolerable community sizes for chimpanzee should be at least 45 individuals as indicated above (Fig. 5), this analysis suggests that no community anywhere in Africa could survive without adopting a fission–fusion social structure. The advantages of fission–fusion lie in reducing the costs of moving and thereby in saving time that can be devoted to feeding and social interaction. Figure 7 illustrates this by depicting moving times as a function of rainfall and party size using the equation in Table 3. Note that when rainfall is low (<1,000 mm, which is insufficient to maintain forest cover) and party size is large (>10 individuals), moving time very quickly becomes prohibitively high. However, when annual rainfall exceeds about 1,000 mm, splitting into smaller parties during foraging reduces moving time to more manageable proportions.

Fig. 6 Boxplots of predicted maximum ecologically tolerable community sizes for chimpanzee communities with and without fission–fusion social structure

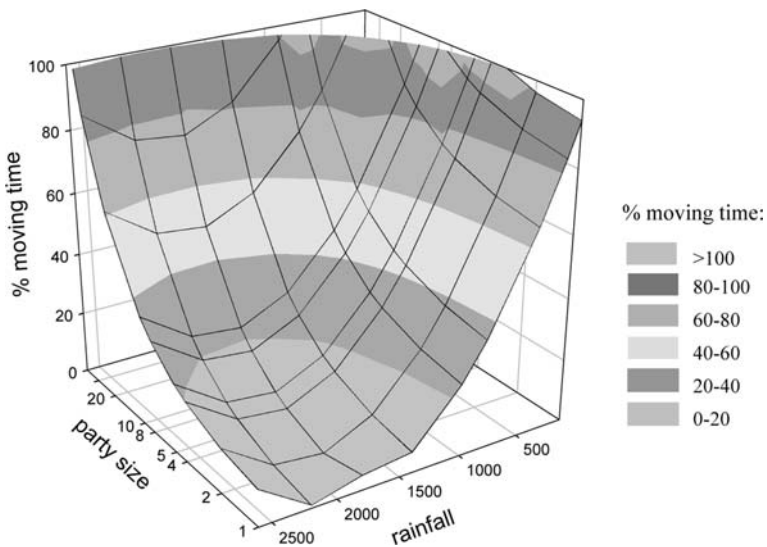
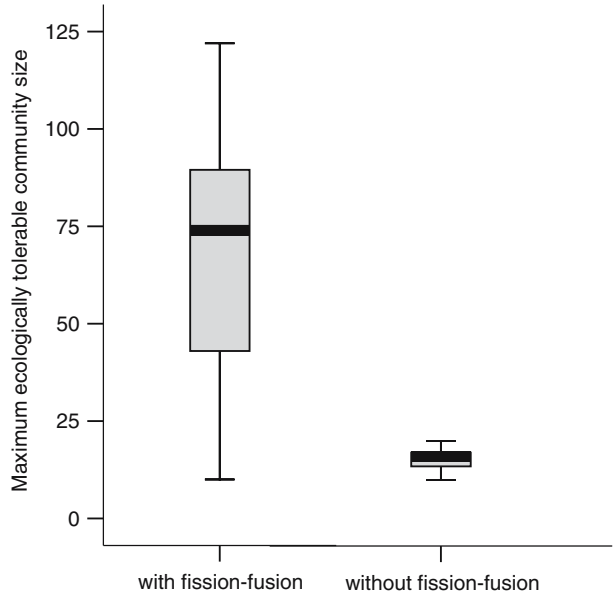


Fig. 7 The effects of subgroup formation on moving time under various rainfall patterns. This figure depicts moving times as a function of rainfall and party size, using the equation in Table 3. *Shadings* indicate areas of similar moving times

Discussion

The model presented here for chimpanzee socio-ecology and biogeography is encouragingly accurate as shown by tests of its ability to predict the presence and absence of chimpanzees across sub-Saharan Africa. It produced only two false

negative predictions, which are at the most (south-)eastern end of the species' distribution and are probably due to an overestimation of moving and resting time. It is likely, that populations at the fringe of the distribution of a species live in less optimal habitat and are under ecological stress. Under such circumstances, populations may be able to survive by making adjustments that save time: as habitat quality deteriorates, for example, baboons travel faster so as to be able to cover longer daily travel distances while holding moving time constant (Dunbar 1992c). Of course, such tactics do not come without a cost, but they may be enough to allow a species to survive on the margins of its natural distribution.

Ecology and biogeography—testing the model

Most of the false predictions produced by the model are false positive predictions: i.e. the model predicts that chimpanzees live in places where they have not been observed. Many of the false positive sites are actually near locations at which chimpanzees do occur, indicating that the general area provides suitable habitat for chimpanzees, even if they do not actually occur at that particular location. It may be, of course, that they did occur there in the historical past. Indeed, recent reports of fossil records of chimpanzees in the eastern rift valley (McBrearty and Jablonski 2005) suggest that the historical distribution of *Pan* extended much further east than previously assumed. Additionally, the climate data for many sites used in this model are extrapolated from weather stations further away or based on a model themselves (e.g. the Willmott and Matsuura database) rather than on observed values. Extrapolations work well to predict the general climatic conditions of an area, but it may produce inaccurate data for specific sites, especially in areas with high mountains or other physical features that affect local climate.

Our model also suggested that chimpanzees should extend much further south than their currently known distribution, including most of Angola into their geographical range (see Fig. 4). Historically, the rainforest belt in this area might have stretched as far as 9° south (Eggert 1992), so *Pan*'s distribution might indeed have stretched much further south than it does now (Myer-Thompson 2003). Note that our model does not differentiate between *P. paniscus* and *P. troglodytes*. *P. paniscus*, however, is usually considered to be more specialized than *P. troglodytes* (but see Thompson 1997) and may require more dense forest or a higher proportion of fleshy fruits to be able to survive. It may be significant that our model fails to predict present day distribution boundaries mainly south of the Congo River, where only *P. paniscus* occurs. Thus, the failure of our model to accurately predict the southern distribution boundary for this species might well be due to the fact that *P. troglodytes* is indeed able to live in this habitat, but not *P. paniscus*. Forest cover south of the known distribution of *P. paniscus* is consistently below 60%, whereas all sites where we know *P. paniscus* is present have forest covers of 60–80% (see also Myer-Thompson 2002). Thus, it seems that, although *P. troglodytes* can survive in habitats with forest covers of only 20%, *P. paniscus* may need more continuous, dense forest. In addition, other substantial rivers such as the Kasai-Sankuru river may limit the southern-most distribution of bonobos (see Eriksson et al. 2004). However, our analyses also suggest an alternative explanation—namely the fact that maximum sustainable group sizes may be too small to support viable chimpanzee communities in these southern locations.

Maximum ecologically tolerable group sizes

In terms of community sizes, our model led to realistic predictions. As required by the logic behind the model, predicted values for community sizes were larger than observed values (Fig. 3), indicating that most chimpanzee populations do not live at (although some may be close to) their maximum ecologically tolerable community size. However, many chimpanzee populations, which now have low community sizes, had much larger communities when they were first habituated and have since declined due to a combination of human encroachment, hunting and epidemic disease (Boesch and Boesch-Achermann 2000; Greengrass 2000; Nishida 1990). The original community sizes typical of most of these communities (80–100 individuals) are very close to the average community size of 77 individuals predicted by our model. The model suggests that it is predominantly feeding and social time that set the upper limit on chimpanzee community size. The largest known chimpanzee community to date has around 150 members (Mitani et al. 2002b), as compared to the largest predicted community of 122 individuals. However, natural communities as large as this are in fact rare, and it is always possible that isolated cases represent instances of communities in the early stages of undergoing permanent fission (as, for example, happened at Gombe during the late 1960s).

The strong relation between community size and feeding time ($r = 0.88$), suggests that feeding time is primarily affected by scramble competition [see also Wrangham 2000 rather than by contest competition]. If contest competition played a stronger role, we should have expected party size to have an effect on feeding time, since it is the members of a party (i.e. the individuals found together at a food patch) that would be in contest with each other. However, we found no such relationship. In addition, observational data suggest that, overall, chimpanzees spend only relatively little time feeding on monopolisable items (e.g. Wittig and Boesch 2003). The fact that it is community size (i.e. the number of individuals sharing the same home range, irrespective of whether or not they are at the same food patches) and not party size that affects feeding time suggests that scramble competition may be the more important factor influencing/limiting chimpanzee community size.

The evolution of fission–fusion

What advantages do chimpanzees gain by living in a fission–fusion society? And why is such a social system not more commonly observed? To understand how such a system could have evolved, we need to understand both the costs that living in a large community imposes on chimpanzees (which force them to split into smaller subgroups) and the benefits that maintaining a large community brings, even though the members of a community are rarely seen all together. It has long been suggested that fission–fusion might serve to overcome the negative consequences of group-living (Kummer 1971). Evidence from a number of sites indicates that party size is related to food availability (Boesch 1996; Chapman et al. 1995; Matsumoto-Oda et al. 1998; Wrangham 1977, 2000; Wrangham et al. 1992, but see also Hashimoto et al. 2001, 2003; Newton-Fisher et al. 2000) and that feeding time varies with party size (Doran 1997; Sakura 1994), suggesting that fission–fusion may serve as a mechanism to reduce within-group feeding competition.

However, these results are not found consistently across populations, and our model shows that the real benefit of adopting a fission–fusion strategy derives from

its effect on moving time, not feeding time (Fig. 6). By reducing moving time, chimpanzees will also reduce their energy demand, thereby further reducing feeding time (see also (Korstjens et al. (2006) for a similar finding in spider monkeys). The advantage of fission–fusion, however, does not lie so much in colonizing new habitats where they could not otherwise survive, but in allowing community size to increase: without fission–fusion the maximum community size would be in the range of 15–20 individuals (close to that observed in gorillas), whereas a fission–fusion strategy allows chimpanzees to live in communities of up to 130 individuals. The advantages gained by living in a larger community may be related to reproductive strategies and/or to territory defence strategies (Lehmann and Boesch 2003; Williams et al. 2004).

In this study, we used a conservative approach and defined a community size of ten individuals to be the smallest possible value for a viable community. In reality, this minimum value is almost certainly much bigger, since most known chimpanzee communities consist of more than ten individuals (also note that predicted maximum ecologically tolerable group size is expected to be larger than observed community sizes). If we assume that the minimum value for a maximum ecologically tolerable community size has to be considerably larger than ten individuals in order to accommodate communities of a viable size (perhaps closer to 45 individuals, as suggested by the bimodal distribution of predicted community sizes), chimpanzees would not be able to survive anywhere in Africa without adopting a fission–fusion social structure. Using fission–fusion as a means of diminishing the costs of group-living is, however, only possible in species where the advantages of living in large groups are not primarily driven by the risk of predation. In species where the main advantage of group-living lies in reducing predation risk, the formation of smaller subgroups would almost certainly enhance predation risk to an intolerable level. Thus, smaller bodied primates usually live in more cohesive groups, which rarely split into smaller subgroups for extended periods of time. Only larger bodied species like chimpanzees and elephants, or carnivores like hyenas that are near the top of the food chain, may be able to survive in small foraging groups.

Furthermore, living in a tightly bonded fission–fusion society may place high cognitive demands on individuals, as each member of the group must be able to keep track of individual relationships even during extended periods of absence of the other group members. This is supported by the fact that this type of fission–fusion is only found in species such as hyenas, dolphins, elephants, chimpanzees and spider monkeys which have larger than average neocortices. Thus, fission–fusion as a solution to intra-community competition may only be an option for species with relatively large brains and in which the main advantage of group-living is not primarily driven by predation pressure.

Conclusions

In conclusion, this study demonstrates that chimpanzee distribution and maximum ecologically tolerable community size can be predicted using the relationships between community size, climate and time budgets. Our model thus provides, for the first time, a clear mechanistic explanation for chimpanzee biogeography. It further suggests that some chimpanzee communities live near their maximum ecologically tolerable group sizes and that the upper limit for chimpanzee community sizes is

constrained by feeding and social time. Further, this study also suggests that the fission–fusion life-style so characteristic of chimpanzees may serve to decrease some of the costs associated with living in large groups (notably moving time). By adopting a fission–fusion social structure, chimpanzees are able to form considerably larger groups which may enable them to live in habitats where they could otherwise not survive. Because chimpanzees (and other large bodied primates, such as humans) are relatively large and consequently suffer less from predation, they can afford to form these much smaller subgroups while still having sufficient protection against predators. Fission–fusion, therefore, is only possible because the advantages of large communities do not lie primarily in protection from predators. Our data thus provide the first evidence for a mechanistic link between fission–fusion social systems and the costs of group-living. Our model also demonstrates how behaviour and social structure shape chimpanzee biogeography, which has important implications for conservation issues. However, more detailed data are needed to fully understand what determines minimum group size in chimpanzees and what benefits they derive from living in large communities. Finally, it is important to remember that these models are taxon-specific: the parameter values for the equations depend on how the species-specific physiology interacts with environmental parameters that influence thermoregulation and nutrient throughput. Consequently, while the general findings will hold across a wide taxonomic range, the precise details and their biogeographic implications will vary from species to species.

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