



Socioecological adaptations by chimpanzees, *Pan troglodytes verus*, inhabiting an anthropogenically impacted habitat

Kimberley J. Hockings^{a,b,*}, James R. Anderson^c, Tetsuro Matsuzawa^d

^a Centre for Research in Anthropology (CRIA)/Faculdade de Ciências Sociais e Humanas, Universidade Nova de Lisboa, Lisboa, Portugal

^b Anthropology Centre for Conservation, Environment and Development, Oxford Brookes University, Oxford, U.K.

^c Department of Psychology, Stirling University, Stirling, U.K.

^d Primate Research Institute, Kyoto University, Kyoto, Japan

ARTICLE INFO

Article history:

Received 27 November 2010

Initial acceptance 22 February 2011

Final acceptance 16 December 2011

Available online 23 January 2012

MS. number: 10-00827R

Keywords:

activity budget

anthropogenic risk

chimpanzee

nutritional advantage

Pan troglodytes verus

party size

Despite the spread of human-impacted wildlife habitats, few studies have examined how animals adapt their socioecology in agricultural–forest ecotones. Anthropogenic processes such as agricultural development directly affect the ecological challenges that species face. In agricultural–forest ecotones cultivated foods that are palatable, energy-rich, easily digestible, and that often occur as large, clumped and spatially abundant orchards or fields may offer foraging advantages over natural foods. However, crop raiding can be risky: harassment, injury or even death may arise from confrontations with people. The factors that affect grouping decisions and activity budgets within anthropogenic environments are unknown. Twelve months of focal data were collected from direct observations of one chimpanzee community inhabiting a forest–farm mosaic at Bossou, Guinea. Wild fruit abundance did not directly influence daily party size. Instead, cultivated resource consumption, in combination with other social factors, provided chimpanzees with an alternative to fissioning. Chimpanzee party size did not differ between crop raids and wild feeds, but party cohesiveness did increase during raids. Furthermore, males and females adapted their activity budgets in different ways to integrate cultivated resources into their broader ecological strategy. As species are increasingly forced into anthropogenically impacted habitats, models of fission–fusion dynamics and other socioecological adaptations need to take into account exploitation of cultivated, energy-rich crops.

© 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Expanding human populations, and in some cases traditional or recent protective measures towards wildlife, mean that many species inhabit increasingly human-influenced landscapes including exceptional proximity to people (Fuentes & Wolfe 2002; Osborn & Hill 2005; Treves 2009; Lee 2010; Strum 2010). Human encroachment poses a major threat to wildlife through indirect causes such as natural habitat destruction and fragmentation (Saunders et al. 1991), or direct human-caused mortality that is often retaliatory in response to crop raiding (animals feeding on foods cultivated by people) or attacks on local persons (Woodroffe et al. 2005; Hockings & Humle 2009; Dunham et al. 2010). As a result, research is increasingly focusing on the biological characteristics that enable a species to respond to direct and indirect anthropogenic threats (Purvis et al. 2000). For example, Fritz et al. (2009) suggested that larger rather than smaller species have

a greater extinction risk from anthropogenic threats, such as habitat loss via land conversion and subsistence hunting, in tropical areas than elsewhere. Larger mammals have larger home ranges so are more likely to encounter human threats, and subsistence hunting, which is largely confined to tropical areas, preferentially targets larger mammals. Owens & Bennett (2000) demonstrated that habitat loss and human persecution had independent effects on the extinction risks of different bird lineages: extinction risk incurred through habitat loss is associated with habitat specialization and small body size, whereas extinction risk incurred through persecution is associated with large body size and long generation time. Isaac & Cowlishaw (2004) showed that terrestrial frugivorous primate species are less vulnerable to local extinction in shifting-agricultural landscapes than arboreal and non-frugivorous species, probably because of the formers' ability to leave forests to exploit more open areas containing cultivated fruiting trees. Anthropogenic processes such as agricultural development directly influence the ecological and social challenges that species face (Fuentes & Hockings 2010). Exactly how wildlife modify their behaviour in response to anthropogenic habitats and

* Correspondence: K. J. Hockings, Departamento de Antropologia, Universidade Nova de Lisboa, 1069-061 Lisboa, Portugal.

E-mail address: hock@fch.unl.pt (K. J. Hockings).

their associated risks (e.g. during crop raids) remains unclear, but is of central concern for the long-term survival of animals whose ranges include such environments (Berger-Tal et al. 2011).

Cultivated Resource Acquisition

Data are accumulating on the widescale consumption of cultivated foods by large mammals (see Naughton-Treves & Treves 2005). Crops are nutritionally important to many species and can contribute a very high proportion of feeding time. For example, at Bossou in Guinea, crops accounted for an average of 8.8% of chimpanzee feeding time (monthly range 1.8–16.6%; Hockings et al. 2009). Furthermore, overall crop-raiding levels by wildlife appear higher when wild fruits are scarce; however, certain crops are frequently raided irrespective of wild fruit availability (Naughton-Treves et al. 1998; Hoare 1999; Osborn 2004; Hockings et al. 2009, 2010a). In agricultural–forest ecotones cultivated foods that are palatable, energy-rich, easily digestible, and often present as large, clumped and spatially abundant crop patches (i.e. orchards or fields) may offer energetic advantages over natural foods (Harris 1970; Forthman-Quick 1986; Terborgh & Janson 1986; Forthman-Quick & Demment 1988; Sukumar 1990; Strum 1994; Saj et al. 1999). According to the model of ecological constraints on animal group size, group size should be strongly correlated with food availability to reduce within-group feeding competition. In fission–fusion species, in which individuals within a group often split into smaller subgroups, large subgroups form to exploit abundant food patches and divide when fruits are scarce, thus reducing the need to travel large distances in search of food (Bradbury & Vehrencamp 1976; Chapman et al. 1995; Janson & Goldsmith 1995; Gillespie & Chapman 2001). Thus, cultivated areas might allow individuals to reduce travel costs and congregate to feed on abundant food sources (e.g. Osborn 1998), showing parallels to what happens during wild fruiting events in which numerous individuals, even those from more solitary species, feed simultaneously at large fruit patches (e.g. Bornean orang-utans, *Pongo pygmaeus*, during Dipterocarp fruiting: Knott 1998; African forest elephants, *Loxodonta cyclotis*, during *Sacoglottis gabonensis* fruiting: Morgan 2009).

Obtaining crops can be risky for crop-raiding animals, even those that are endangered and legally protected, owing to harassment, injury or even death during confrontations with people (Reynolds 2005; Strum 2010). This appears especially so for large-bodied and cognitively advanced species such as elephants and great apes; not only can these species adapt flexibly to anthropogenic changes to their environment, but they are also increasingly cited as posing a threat to human safety (Hoare 1999; Hockings & Humle 2009). Crop raiding by elephants is predominantly a nocturnal behaviour (Bell 1984; Thouless 1994; Hoare 1995), 'suggesting that offenders seek to minimize the associated risk' (Hoare 1999, page 690). Ahlering et al. (2011) reported higher levels of stress hormones (glucocorticoids) in crop-raiding elephants than those in protected areas and suggested that real or anticipated attacks by humans during crop raids were likely to be stressful. When feeding on crops instead of wild foods, chimpanzees at Bossou showed increased anxiety-related behaviours including rough self-scratching (Hockings et al. 2007). Bossou chimpanzees also vocalized less when feeding on raided food, presumably to reduce detection by farmers. Females showed the greatest reduction in vocalizing, consistent with their being more afraid than males during raids (Hockings 2007). Likewise, the chimpanzees transported more food when feeding on crops; by taking food to relatively safer locations they reduced the amount of time spent in an exposed area, and thus the likelihood of detection by people (Hockings 2007).

Adaptations to Anthropogenic Habitats

Behavioural flexibility confers important fitness benefits in seasonal, novel or altered environmental situations (Reader & MacDonald 2003; Sol 2003; Sol et al. 2005). However, data on flexibility of animals' grouping dynamics in anthropogenic habitats are scarce. Wilson et al. (2007) compared the behaviour of chimpanzees (Kibale, Uganda) in what they described as two potentially dangerous situations: adult males conducting border patrols at the periphery of their home range, and when entering croplands to feed. They concluded that chimpanzees modified their grouping behaviour by increasing the number of adults in a party in areas with a high risk of detection. They suggested that larger groups were advantageous in croplands by decreasing individuals' need for vigilance, and these larger groups emerge from reduced within-group feeding competition owing to the clumped distribution of crops. Although there is debate about the extent to which aggregations in primates are an antipredator strategy (see Cowlishaw 1999 for an overview), Bettridge et al. (2010) demonstrated, using time budget models, that minimum group size in wild-ranging baboons (*Papio* spp.) is related to predator density and female body mass. Robinson (1981) also showed that close neighbour proximity (around 5 m or less) could reduce an individual's perceived predation risk (recorded through increased vigilance) in capuchin monkeys, *Cebus nigrivittatus*. In heavily human-influenced habitats, large predators are often hunted and exterminated by humans, consequently removing the threat of predation to sympatric prey species. Nevertheless, the effects of human confrontation on perception of risk in anthropogenic habitats may function in the same way as predation, with individuals preferring to remain in larger parties in locations where degree of risk is elevated, such as in cultivated areas.

Access to human food clearly impacts on animals' activity budgets; it has resulted in a higher proportion of time resting and a lower proportion of time feeding in baboons, and vervet monkeys, *Chlorocebus aethiops* (Strum 1984, 2010; Saj et al. 1999). However, Campbell-Smith et al. (2011) found that both food availability (wild and cultivated combined) and crop raiding strongly influenced orang-utan, *Pongo abelii*, ranging strategies, with individuals travelling further on crop-raiding days than on days when only wild fruits were consumed. In a comparative study between groups of human-commensal and wild-foraging white-faced capuchins, *Cebus capucinus*, at Curú in Costa Rica, little difference was found in activity budgets (McKinney 2011). We would also expect that individuals requiring the greatest nutritional intake (i.e. females engaged in costly reproductive effort) might show more reliance on crops especially during periods of wild food scarcity, given that under good nutritional conditions female primates live for longer, reproduce at an earlier age and have a higher rate of reproduction (Key & Ross 1999). In agreement, Strum (2010) showed that crop-raiding baboon females reproduced faster and at an earlier age and had shorter interbirth intervals than nonraiding baboons. However, studies also show that females, especially those with dependent offspring, are often less willing to exploit human crops than males (*Papio anubis*: Strum 1984; *Macaca ochreata brunneescens*: Priston 2005; *C. aethiops*: Saj et al. 2005; *P. troglodytes verus*: Hockings et al. 2007; but see Campbell-Smith et al. 2011 for an exception in *P. abelii*). Likewise, male Asian elephants, *Elephas maximus*, were significantly more likely to raid crops than females, and it was proposed that this is a high-risk strategy by males to maximize reproductive success through improved nutrition, a strategy that females are less likely to adopt (Sukumar & Gadgil 1988; Sukumar 1991).

Chimpanzees provide an appropriate model species to test socioecological adaptations to anthropogenic habitats as they (1) exhibit

ecological flexibility that allows them to exploit areas of human agricultural development (Yamakoshi 1998), (2) occur extensively in areas of anthropogenic influence throughout Africa (Tweheyo & Lye 2005; McLennan 2008; Hockings & Humle 2009; Hockings et al. 2009), and (3) exhibit fission–fusion dynamics (Nishida 1968) which allows responses to social and ecological change to be assessed over very short timescales (Aureli et al. 2008).

The diet of wild chimpanzees is dominated by ripe fruit, which, irrespective of the chimpanzees' environment, accounts for 50–75% of overall feeding effort (Wrangham 1977; Goodall 1986; Tutin et al. 1997; Pruett 2006). Some research suggests that chimpanzee party size increases during periods of high fruit availability (Chapman et al. 1995; Boesch 1996; Wrangham 2000). However, other factors also influence subgroup (or party) size, including social factors such as the presence of sexually receptive females, demographic factors such as community size and sex ratio, and potential threats including predators (Goodall 1986; Boesch & Boesch-Achermann 2000; Newton-Fisher et al. 2000; Hashimoto et al. 2001, 2003; Anderson et al. 2002; Mitani et al. 2002; Reynolds 2005). Lehmann et al. (2007) proposed a taxon- and habitat-specific time budget model to demonstrate that fission–fusion dynamics can decrease costs, particularly travelling time, associated with living in large groups. However, studies of animal groups living in 'natural' environments show variable associations between food availability, subgroup size and travel costs (Wrangham 1977; Symington 1988; Doran 1997; Asensio et al. 2009), with ecological factors sometimes influencing age and sex classes differently (Chapman et al. 1995). In view of their importance, quantitative data on socioecological factors that underlie grouping decisions and activity budgets in both cropland and wild habitats are surprisingly scarce.

Our aim in this study was to investigate how wild food availability, crop consumption (incorporating the effects of resource competition and increased perception of risk) and other social factors (such as the presence of a maximally sexually receptive female) interact to affect fission–fusion dynamics and activity budgets in a wild chimpanzee community inhabiting a forest–farm matrix. We tested the following hypotheses.

(1) As chimpanzees can feed on crops during periods of wild fruit scarcity they do not need to split into smaller parties; thus party size will not vary in response to wild food availability but chimpanzees will raid crops when parties are large and this will be influenced by social factors.

(2) If feeding party size and cohesiveness are affected by crop raiding, then larger and more cohesive parties (as indicated by decreased party spread and increased interindividual proximity) will occur when chimpanzees raid crops compared to wild feeding owing to low feeding competition and benefits of overall increased vigilance, as crop raiding is associated with heightened perceived risk.

(3) If daily activity patterns are affected by crop raiding, then crop raiding will result in increased time resting and reduced time feeding, as in other primate species (Strum 1984; Saj et al. 1999), because of nutritional advantages.

(4) If activity budgets are impacted by sex class, then increased boldness and a greater willingness to raid will mean that activity budgets of males are influenced more by crop raiding than those of females.

METHODS

Study Site and Subjects

The village of Bossou is situated in the forest region in south-eastern Republic of Guinea, West Africa (7°38'71.7"N, 8°29'38.9"W), approximately 6 km from the Nimba Mountain range (see

Matsuzawa et al. 2011). The village is mainly inhabited by the Manon ethnic group. The Manon family that founded Bossou still remains one of its most influential families and holds the sympatric chimpanzees as a sacred totem (Yamakoshi 2011). Owing to these local cultural beliefs humans and chimpanzees have coexisted in close proximity over many generations. However, in recent years, aspects of development, various socioeconomic factors, such as reliance on a cash income from crop sales, and variations in the chimpanzees' behaviours, including crop raiding and attacks on people, have altered the relationship dynamics. People often behave aggressively and throw stones in an effort to displace the chimpanzees (Hockings et al. 2010b), and the chimpanzees show more behavioural indicators of anxiety when crop raiding than wild feeding, including rough self-scratching (Hockings et al. 2007). The forests currently sustain no large predators as a result of past hunting activities by local people (Sugiyama 2004) and there are no adjacent neighbouring chimpanzee communities. The hills that constitute the chimpanzees' 15 km² home range (7 km² core area) are bisected by roads (Hockings et al. 2006) and covered in primary and secondary forest. Swidden (or 'slash-and-burn') agricultural practices have resulted in a mosaic of thicket, cultivated fields and orchards within and bordering the reserve. The climate at Bossou is classified as tropical wet seasonal; there is a clear wet season from March to October and a dry season from November to February (Takemoto 2004; Hockings et al. 2009).

In addition to wild foods, Bossou chimpanzees consume 17 different types of cultivated foods (Hockings et al. 2009). Crops are defined as those that are at least periodically guarded by humans; thus a crop-raiding 'event' was defined as any successful foray to obtain guarded cultivated food (Naughton-Treves et al. 1998). Abandoned orchards and fields were never guarded by farmers and acquisition of these foods was not considered to be crop raiding; therefore specified abandoned crops were analysed separately from crops and wild foods. Oil-palm fruits and nuts, *Elaeis guineensis*, and coula nuts, *Coula edulis*, were supplied by researchers for short periods during January and December (months of wild fruit abundance) for nut-cracking experiments (see Carvalho et al. 2008). Neither supplied foods nor abandoned crops were associated with human risks, and are thus analogous to wild foods. The two crop conditions (i.e. crops and abandoned crops) allow us to differentiate between effects of perceived risk and effects of energetics and competition on chimpanzee behaviour. Although like wild fruits, various crops, including those from abandoned sources, were seasonal (Hockings et al. 2009), they were generally available year-round, and were usually found in distinct and clumped areas of varying size within the chimpanzees' home range (as seen in Fig. 1).

Owing to the emigration of an adult female and her infant, and one birth, group size varied over the study period from 12 to 14 individuals, with five to six adult females and the same three adult males present throughout. There were three juveniles and one to two infants; individuals below 8 years old were classified as immature.

Data Collection

Behavioural observations

Behavioural data were collected over 12 months (specifically, during every month of the year in three periods between May 2004 and December 2005), and phenological data were collected continually over the 20 months. A focal adult (all immatures were excluded) was randomly selected from a predetermined list each day and when possible followed from 0630 hours to nesting. Each individual was sampled twice per month when possible, and a total of 187 adult focal samples were thus collected (13–17 focal days/

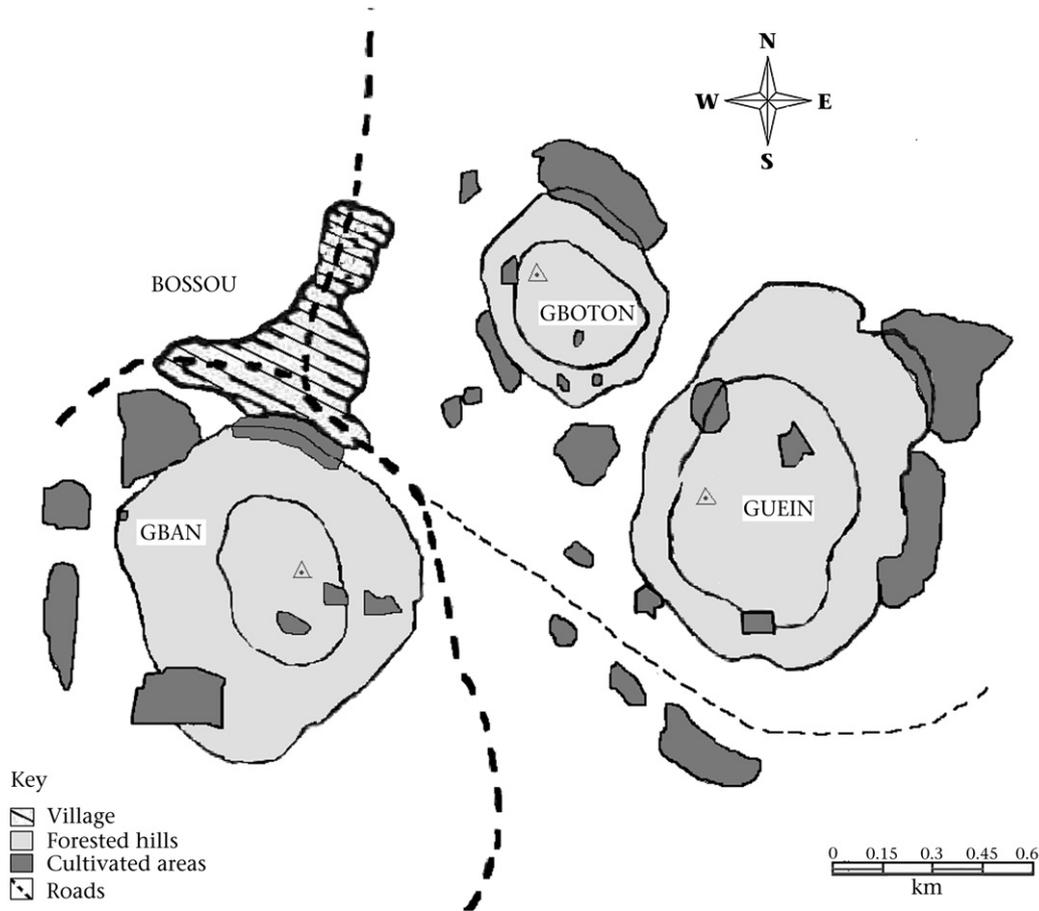


Figure 1. A map of the study site (Bossou), showing the village, the roads (dashes) and the three main forested hills that constitute the chimpanzees' core range area. The presence of human-guarded cultivated areas within and surrounding the chimpanzees' core area in 2005 are highlighted in dark grey.

month; mean daily observation time per individual \pm SD = 8.95 ± 2.37 h), totalling 1673 h of observations. From the 187 focal samples, days with ≥ 5 h of observation time (full-day observations: mean \pm SD = 9.56 ± 1.46 h, $N = 169$) were selected for specified analyses (see *Data Analyses* section); mean focal observation times of adult males and females were very similar (male: mean \pm SD = 9.92 ± 1.29 h, $N = 58$; female: mean \pm SD = 9.38 ± 1.52 h, $N = 111$).

Every 5 min instantaneous sampling was used to record the ongoing behaviour of the focal individual (Martin & Bateson 1986). Behaviours were divided into four main categories: feeding, moving, resting and social (Lehmann et al. 2007; for chimpanzee ethogram, see Nishida et al. 1999). While the focal individual was being followed, after each focal point entry, records were made of all other individuals present, group spread and proximity of the nearest neighbour. For two reasons, a party was classified as all individuals within a 30 m radius from the focal individual and excluded dependent infants (adapted from Sugiyama & Koman 1979; Sakura 1994; Bates & Byrne 2009). First, beyond 30 m visibility was restricted. Second, Bossou is mostly composed of regenerating secondary forest and the vast majority of trees are less than 20 m in height (Hockings 2007), so even if one individual was arboreal and another terrestrial, the 30 m measure would still be suitable. This method ensured that party sizes associated with focal adults and between wild/cultivated areas were equally represented. All scan data collected during focal follows were used in analyses of party size. Party spread and nearest-neighbour proximity were recorded on the 5 min mark. Party spread was defined

as the furthest estimated distance (m) between two individuals within the party, and 'proximity of nearest neighbour' was the distance (m) between the focal individual and the chimpanzee nearest to it (excluding dependent infants). It should be noted that members of a party were not always engaged in the same behaviour as the focal individual.

Distance estimation tests were conducted three times by K. H., once at the beginning of each data collection phase. K. H. estimated 10 arboreal and 10 terrestrial distances in different types of forest and in more open areas; these were subsequently measured. There were no significant differences between actual and estimated distances in any of the three periods (paired-sample t test: May 2004: $t_{19} = 1.00$, NS; January 2005: $t_{19} = 0.24$, NS; November 2005: $t_{19} = 1.00$, NS).

Phenological surveys

A total of six transect lines (total distance 4739 m) were set up to monitor all trees and lianas (total of 3611 trees/lianas) in the three principal hill forests of Bossou, namely Gban, Guein and Gboton. Each transect line was 10 m wide, and included every tree or liana greater than 5 cm in diameter at breast height. The transects were made in north-to-south and east-to-west directions from the summit of each hill until reaching a road or cultivated field (north-to-south and east-to-west directions, respectively: Gban: 1110 m: 811 trees and lianas; 976 m: 792 trees and lianas; Guein: 870 m: 530 trees and lianas; 900 m: 722 trees and lianas; Gboton 424 m: 314 trees and lianas; 459 m: 442 trees and lianas). Transects passed through all the habitat types present in the home range, and

the trees and lianas sampled are considered representative of the local flora. However, cultivated fruit orchards were not present on transects and, as a result, cultivated fruit is not included in this measure of habitat-wide fruit availability. Transects were monitored during the 2nd and 4th week of each month, and each tree or liana was scored for ripe fruit availability as follows: 0: absent; 1: 1–25% of canopy cover; 2: 26–50% cover; 3: 51–75% cover; 4: 76–100% cover. The following formula was used to calculate the fruit availability index (FA index), which assumes a circular cross-section of trunks (modified from Takemoto 2004):

$$\text{FA index} = \left[\frac{\sum (P_i \times F_i)}{\sum (P_i \times 4)} \right] \times 100$$

where P_i is the basal area of the tree (cm^2), and F_i is the fruiting score of the tree (0–4). ‘Chimpanzee food species’ are defined as those fruit species that K. H. observed chimpanzees consuming during the study period, and were used for subsequent calculations of wild fruit availability (using a total of 1596 trees from 59 species).

From phenological data collected, months of high wild fruit availability were December to April, whereas low fruit availability months were May to November (see Fig. 2; FA index values: mean \pm SE, high versus low = 4.8 ± 0.6 versus 1.4 ± 0.1). These distinctions between high and low wild fruit availability seasons are used in subsequent analyses.

Data Analyses

As chimpanzees often transported arboreal crops to a terrestrial location (Hockings et al. 2007), only arboreal spread and proximity feeding data (for wild foods, crops and abandoned crops) were analysed (see Cowlshaw 1999). Spread and proximity data for (1) wild foods and crops and (2) wild foods and abandoned crops were compared within each day using a paired t test, with effect sizes calculated using the Pearson correlation coefficient r (Cohen 1992). For example, if focal individual A fed on both crops and wild foods within a day, then two data points (one matched pair) were generated individually for average spread and average proximity.

As focal chimpanzees fed arboreally on both crops and abandoned crops on the same day on only two occasions, analyses comparing these two conditions were not possible. Although the canopy sizes and densities of wild trees vary extensively, cultivated trees and abandoned cultivated trees present at Bossou are more comparable as they tend to be similar in size and/or occur in dense patches in orchards often with overlapping canopies owing to human planting practices (Hockings et al. 2009). Furthermore, as chimpanzees within a party were not always engaged in the same behaviour as the focal individual (in this context, feeding) or located in the same feeding tree, these measurements provide an overall indication of the cohesiveness of a party.

Full-factorial ANCOVA models were used to assess changes in average party size per day (or daily party size) as a function of wild fruit availability (high or low), sex class (male or female focal days), reproductive state (the presence or absence of a maximally swollen female in the community), consortship (whether or not a male and female consorted) and crop raiding (whether a crop was consumed or not by the focal individual on that day), with maximum community size as a covariate (as this changed throughout the study period). In line with previous studies on crop raiding by apes (e.g. Campbell-Smith et al. 2011), comparisons between crop-raiding and noncrop-raiding days were considered the appropriate level of analysis. Time spent feeding on crops was not used in analyses of party size as food was often transported back to the forest for consumption, and this measure does not take account of other potentially influential factors such as crop processing requirements or feeding rates, or anthropogenic factors such as human arrival.

From days with ≥ 5 h of observation time, daily changes in behavioural categories (daily percentage of time feeding, travelling, socializing and resting) were analysed as a function of sex class, wild fruit availability, reproductive state and crop raiding using a MANOVA. Linear regression was used to test for a relationship between travel and party size, using daily travel (calculated as a percentage of total activities) against daily mean party size. As absolute travel time (min) per day varied with daily observation

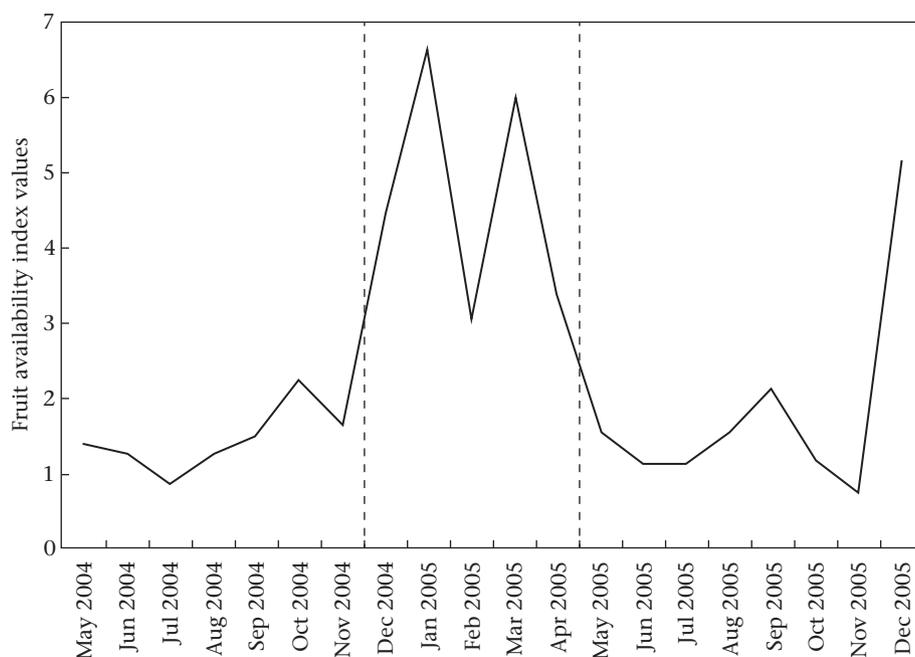


Figure 2. The monthly availability (FA index) of ripe fruit in chimpanzee food species in 2004 and 2005. Dashed lines show divisions between months of wild fruit scarcity and abundance.

times, only days with ≥ 9.56 h of observation time ($N = 100$; mean full-day observation time) were analysed.

All data were analysed using PASW version 17 (SPSS Inc., Chicago, IL, U.S.A.), and were normally distributed with homogeneity of variance (Sokal & Rohlf 1995). All the hypotheses considered were two tailed and tested at $\alpha = 0.05$.

RESULTS

Ecological and Social Factors Affecting Party Size

Daily mean party size \pm SD (all behavioural activities combined) over the study period was 5.0 ± 2.08 individuals. There was a significant interaction between crop raiding and female sexual receptivity on party size ($F_{1,158} = 4.21$, $P = 0.042$; Fig. 3); party size was higher on crop-raid days but only in the presence of a maximally swollen female. Party size decreased when a consortship was in progress ($F_{1,158} = 20.21$, $P < 0.001$). There was a nonsignificant main effect of sex on party size: parties tended to be larger on male than female focal days ($F_{1,158} = 3.35$, $P = 0.069$). Daily party size was not affected by other factors, including degree of wild fruit availability ($F_{1,158} = 0.76$, $P = 0.39$).

Crop Raiding, Party Size and Cohesiveness

Feeding party sizes per day (arboreal and terrestrial combined) tended to be slightly larger when focal individuals fed on crops rather than on wild foods (mean individuals \pm SE = 5.2 ± 0.33 versus 4.7 ± 0.21), but this difference was not significant ($t_{81} = -1.85$, $P = 0.069$) and the effect size was small ($r = 0.04$). No difference in feeding party size per day was observed when individuals fed on abandoned crops rather than on wild foods (mean individuals \pm SE = 5.0 ± 0.45 versus 5.1 ± 0.34 ; $t_{30} = 0.21$, $P = 0.90$). Mean arboreal party spread was reduced when feeding on crops compared to wild foods (9.7 m versus 18.5 m: $t_{20} = 4.58$, $P < 0.001$; Fig. 4) and the effect size was large ($r = 0.51$). Chimpanzees maintained closer proximity when feeding on crops (4.1 m versus 6.3 m: $t_{24} = 2.06$, $P = 0.05$), although the effect size was small ($r = 0.15$). In contrast, no significant differences emerged when party spread (16.3 m versus 18.4 m: $t_{14} = -0.87$, $P = 0.397$) and proximity (6.5 m versus 4.4 m: $t_{15} = 1.79$, $P = 0.094$) were compared during arboreal wild feeds and abandoned crop feeds.

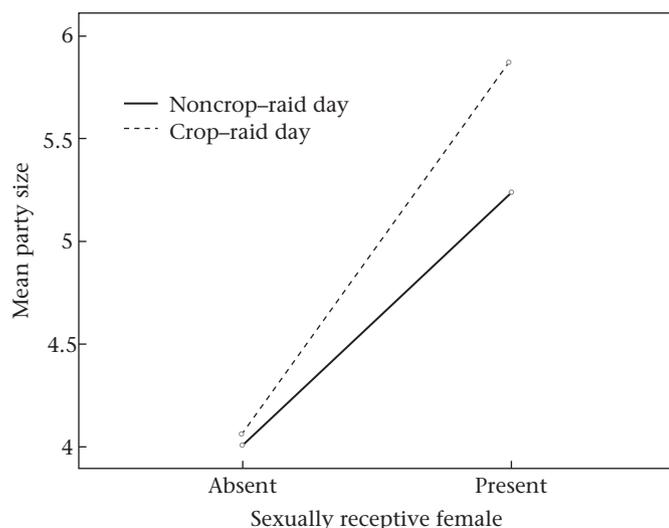


Figure 3. The effect of crop raiding and female sexual receptivity and their interaction on party size. To show the interaction effect data are presented on line graphs.

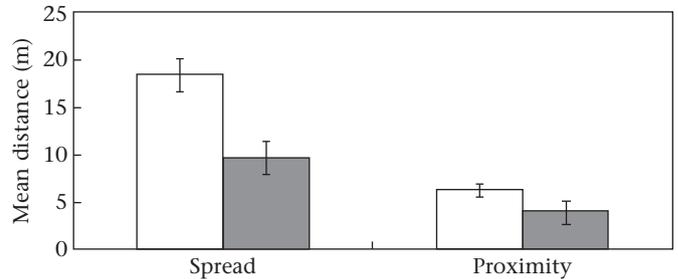


Figure 4. The mean \pm SE party spread and proximity of nearest neighbours when feeding in arboreal wild (white bars) and crop-raid (grey bars) conditions.

Daily Activity Patterns and Sex Class

Bossou chimpanzees spent on average 22.5% of daily observation time feeding, 19.5% travelling, 5.6% socializing and 52.4% resting. Activity budgets were affected by season (Pillai's trace: $V = 0.0086$, $F_{4,150} = 3.519$, $P < 0.01$), crop raiding ($V = 0.163$, $F_{4,150} = 7.516$, $P < 0.01$), sex ($V = 0.181$, $F_{4,150} = 8.306$, $P < 0.01$) and sexual receptivity ($V = 0.101$, $F_{4,150} = 4.226$, $P < 0.01$). Separate univariate ANOVAs revealed that chimpanzees engaged in more travelling, feeding and social behaviour and less resting behaviour on crop-raid than noncrop-raid days (travelling: $F_{1,153} = 5.373$, $P = 0.022$; feeding: $F_{1,153} = 4.053$, $P = 0.046$; socializing: $F_{1,153} = 16.435$, $P < 0.001$; resting: $F_{1,153} = 22.914$, $P < 0.001$; Fig. 5), and spent more time travelling during periods of wild fruit abundance ($F_{1,153} = 4.507$, $P = 0.035$) and less time feeding during fruit scarcity ($F_{1,153} = 8.067$, $P = 0.005$). Males engaged in more social behaviour such as grooming when there was a maximally swollen female in the party ($F_{1,153} = 6.708$, $P = 0.011$). Furthermore, there was a significant interaction between wild food availability, sex and crop raiding ($F_{1,153} = 4.08$, $P = 0.045$; Fig. 6). Specifically, when wild fruit was scarce males spent significantly less time resting when crops were consumed, whereas in general females spent less time resting when crops were consumed regardless of wild food availability. Party size had no effect on daily travel as a proportion of the focal individual's activity budget ($R^2 = 0.0$, $t = 0.072$, $N = 187$, $P = 0.942$) or absolute travel time ($R^2 = 0.001$, $t = -0.351$, $N = 100$, $P = 0.726$).

DISCUSSION

The social organization of a species should be understood as a trade-off of species-specific requirements in a particular habitat

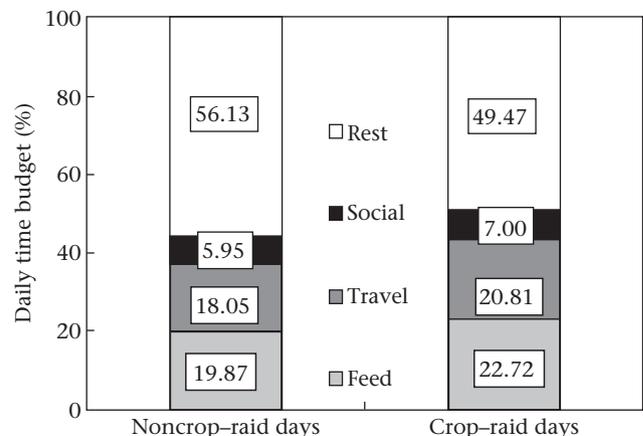


Figure 5. Daily time budgets of noncrop-raid days ($N = 92$) and crop-raid days ($N = 77$). Histogram shows percentage of time engaged in each activity.

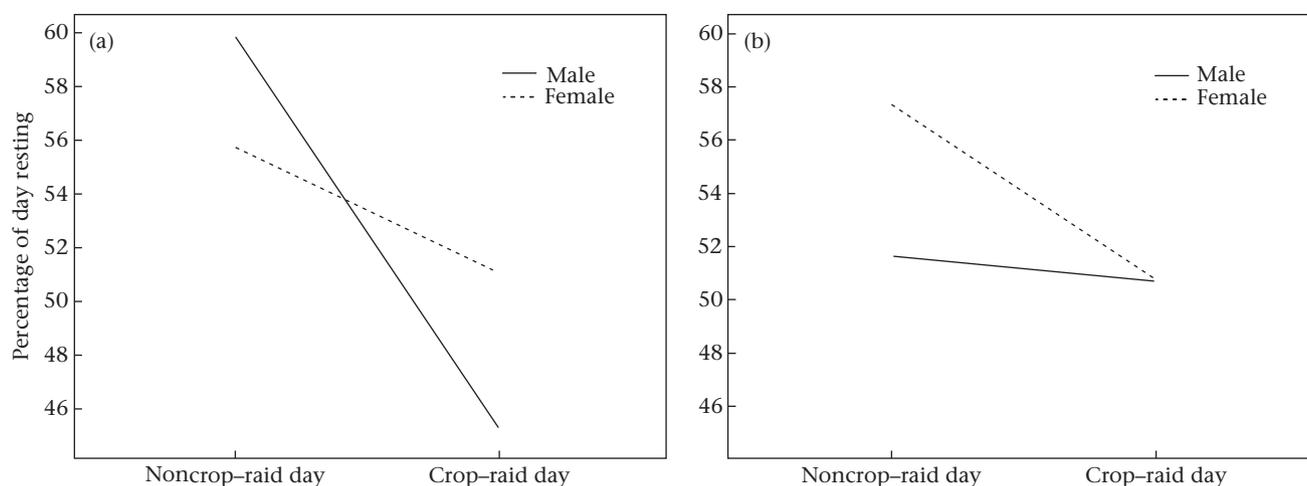


Figure 6. The effect of crop raiding and sex and their interaction on the percentage of the day spent resting during periods of (a) low and (b) high wild fruit availability. To show the interaction effect data are presented on line graphs.

(Dunbar et al. 2009), including anthropogenic environments. As at least some cultivated resources are available year-round at Bossou and chimpanzees can feed on crops during periods of wild fruit scarcity (Hockings et al. 2009), we predicted that unlike other communities, chimpanzees at Bossou do not need to split into smaller parties when wild fruits are scarce. In agreement with hypothesis 1, wild fruit availability did not appear to influence the fission–fusion nature of chimpanzees at Bossou. Instead, chimpanzees raided crops when party size was larger, but only when a maximally swollen female was present. It is possible that this interaction reflects male mate guarding (and a desire for males in general to remain in proximity to the female) during periods of female sexual receptivity, with associated perception of increased security by party members and increased energetic demands by females during these periods (Anderson et al. 2006). Males might be more willing to engage in risky raids when other males are present in larger party sizes for support, or ‘show off’ their boldness to females through crop raiding during these periods (Hockings et al. 2007). These results give support to the ecological constraints hypothesis (Chapman et al. 1995), as crop raiding, in combination with social factors, provides individuals with an alternative to fissioning into smaller parties in response to wild fruit scarcity. Party size decreased when consortships took place, as would be expected in a small community. At these times, adult males appeared to search for the consort while females tended to disperse.

If party size and cohesiveness remain constant when feeding on wild food and abandoned crops it is likely that within-group feeding competition does not differ between wild or crop food sources. Consequently, if party size and cohesiveness increase when feeding on crops compared with wild foods, then it is likely that increased perception of risk is responsible. Our results show that feeding party size did not differ between abandoned and wild feeds or between crop raids and wild feeds, making it difficult to understand fully the complex interaction between perceptions of risk and feeding competition on the decision about whether to raid. However, party cohesiveness did increase when feeding on raided compared to wild foods, but not when feeding on abandoned versus wild foods. This suggests that the degree of perceived risk associated with crop raiding is the most likely explanation and dominant individuals were probably more tolerant of others feeding in direct proximity to them when crop raiding than when feeding on wild foods.

Bettridge et al. (2010) proposed a time budget model to demonstrate that mean group size in baboons increased with

predation risk, with individuals potentially prioritizing survival (over fecundity) in habitats in which predation risk is very high. Our results partially support the idea that perception of risk from human confrontation may function in a similar way as predation risk, with individuals preferring to enter anthropogenic areas to raid crops on days when parties are larger, and feeding parties remaining more cohesive during crop raids than wild feeds. In agreement, unhabituated chimpanzees at Bulindi in Uganda show increased cohesiveness (larger nest groups) when forest fruit is scarce, which might be related to habitat use and foraging strategies at that time, particularly a sharp rise in crop raiding, which increased chimpanzees’ proximity to humans and the risk of hostile encounters (McLennan 2010).

It is unlikely that vegetation structure, canopy size or food density caused differences in cohesiveness in the two crop conditions but future studies should attempt to make more detailed structural comparisons between wild and cultivated food trees, including measures such as diameter at breast height, as patch size impacts grouping patterns in fission–fusion species (Chapman et al. 1995). Future analyses should also focus on crop-raiding bouts and test exactly how the constraints and advantages associated with agricultural areas might influence which individuals choose to raid crops to provide a more precise understanding of wildlife grouping patterns in anthropogenic habitats. For this purpose, variations in human guarding behaviour (Osborn & Hill 2005), in geographical features of an anthropogenic habitat (such as degree of cover, distance between forest edge and field) and in crop availability (size, density and distribution) between fields should be quantified to differentiate more accurately between the effects of degree of anthropogenic risk and within-group competition. Certain crops occur in very large, nondepleting patches (e.g. rice, *Oryza* spp., pith (see Fig. 7) and cassava, *Manihot esculenta*, tuber, see Hockings et al. 2010a). This should allow direct comparisons of within-group feeding competition with other crops that occur in depleting patches (e.g. maize, *Zea mays*), and with wild foods such as monodominant patches of terrestrial herbaceous vegetation of the families Marantaceae and Zingiberaceae (Stephens & Krebs 1986; Chapman et al. 1995). Mapping the distribution and quality of both wild foods and crops would lead to a more inclusive description of spatiotemporal variations in food availability in an animal’s habitat.

The average party size of chimpanzees at Bossou does not vary greatly from other chimpanzee communities inhabiting less human-impacted habitats, despite their small community size



Figure 7. A chimpanzee party feeding on rice pith in a cultivated field. Photo: B. Zogbila.

(mean party size at Bossou 5.0 individuals versus mean party size at seven sites \pm SD 6.7 ± 2.4 individuals; range 4.7–11.2; mean community size \pm SD 65.7 ± 31.2 , range 28–120; data presented in Lehmann et al. 2008). The risks associated with exploiting anthropogenic parts of their habitats might limit individuals' willingness to split into smaller parties (see Sakura 1994). However, it is also possible that the Bossou chimpanzee community shows reduced fission–fusion events compared with other communities owing to its small size (as proposed by Lehmann & Boesch 2004). Moreover, since research began no females have successfully immigrated into the community; the resulting high degree of relatedness among individuals (Sugiyama 2004; Shimada et al. 2009; Matsuzawa et al. 2011) provides an additional social explanation for low fission–fusion dynamics.

As in other primate species inhabiting anthropogenic habitats (e.g. baboons: Strum 1984; vervets: Saj et al. 1999), we predicted that crop raiding would result in increased time resting and reduced time feeding in chimpanzees at Bossou, because they could quickly satisfy their daily nutritional requirements allowing more time for rest. However, like more general time budget models (e.g. Lehmann et al. 2007; Dunbar et al. 2009; Korstjens et al. 2010), our site-specific results highlight the complexity with which different activity budget components influence each other. Contrary to predictions, on crop-raiding days chimpanzees converted resting time (mostly a source of 'uncommitted time' in nonfolivorous primates: Korstjens et al. 2010) to spend a greater proportion of their day travelling, feeding and socializing. It is likely that individuals travelled more for the purpose of crop raiding, fed more because of the availability of clumped crops, socialized more as a result of increased energy levels gained from consuming crops, and consequently rested less. It has been suggested that the main benefit from adopting a fission–fusion society specifically derives from its effects on moving time (Korstjens et al. 2006; Lehmann et al. 2007), and in chimpanzees and spider monkeys (*Ateles* spp.) reduced moving time diminished energy demands and feeding time. Our results also suggest a positive link between these two time budget components whereby increased moving time boosted energy demands resulting in increased feeding time. As groups did not fission in response to wild food scarcity and chimpanzees raided crops when parties were large, party size was not correlated with travel. In addition to climatic conditions, enforced resting time requirements in primates are somewhat set by the time required for digestion, mostly for leaf fermentation (Korstjens et al. 2010). As chimpanzees are highly frugivorous, fruits are mainly targeted in crop raids (Hockings et al. 2009). Thus, during wild fruit scarcity, individuals inhabiting

anthropogenic habitats can exploit fruit crops as opposed to regular lower-quality fall-back foods such as terrestrial piths and leaves (Wrangham et al. 1991); this might result in a short-term reduction in enforced resting time in this species.

The two sexes adapted their activity budgets in different ways to integrate crops into their broader ecological strategy. We predicted that increased boldness and a greater willingness to raid would mean that activity budgets of males would be more greatly influenced by crop raiding than those of females. When wild fruits were scarce, males showed a considerable reduction in resting time on crop-raiding days. This strongly suggests that male chimpanzees choose to raid high-quality crops instead of resting especially during periods of fruit scarcity. Females were more consistent and reduced resting on crop-raid days, but to a lesser extent than males, regardless of wild fruit availability. If management strategies hope to reduce crop-raiding levels by behaviourally flexible species, then approaches to discourage individuals, especially males, from seeking out crops during periods of fruit scarcity (instead of conserving energy through increased rest) will have to be developed. This might be achieved through removal of heavily targeted crops that are available during periods of fruit scarcity or increasing the degree of perceived anthropogenic risk associated with raiding during these periods, for example through more intense guarding in known crop-raiding hotspots or land-use changes such as creating a large clear buffer between the forest edge and crop field (see Hockings & Humle 2009 for a thorough discussion of conflict mitigation techniques).

Bossou chimpanzees may provide a valid long-term demographic, behavioural and ecological template for future chimpanzee communities inhabiting forest–farm matrices (i.e. small community size, high dependence on crops and male-dominated raiding behaviour: see McLennan 2008; Reynolds et al. 2003), but it is interesting to speculate about the picture with larger communities, especially those with more adult males. As tolerance by farmers towards crop raiding diminishes, it is likely that perception of risk by individuals, especially females and immatures, will increase, resulting in predominantly multimale raiding parties. Males may increasingly choose to raid crops instead of resting, especially during periods of wild food scarcity, whereas females might opt for more resting time instead of very risky raids. In the event of continued human tolerance, diminishing wild food availability (because of increased human activities) and increasing crop availability may result in larger raiding parties, dependent on the number of males in the community. Although large chimpanzee communities are unlikely to flourish in very heavily anthropogenically impacted and fragmented landscapes, and a human 'tolerance threshold' towards crop raiding probably exists, these ideas could be tested around the edges of National Parks for example (Hockings & Sousa 2011).

For comparative analyses of species' extinction risk it is important to understand the biological traits that enable species to adapt to anthropogenic habitats. However, when it has been determined that a species can persist in anthropogenic habitats, it is imperative to explain how they do so. It is this behavioural information that will directly inform species-specific conflict mitigation techniques. In conclusion, access by wildlife to cultivated foods can change the challenges of energy acquisition and expenditure, and as species are increasingly forced into anthropogenically impacted habitats, access to energy-rich crops should be incorporated into models of socioecological adaptations to environments.

Acknowledgments

Thanks to the DNRST and S. A. Gaspard, Director of the IREB, Guinea. We also thank the local assistants for their invaluable help

and Bossou villagers for continuing support. We are grateful to two anonymous referees and F. Berkovitch, S. Carvalho, V. Fishlock, T. Humle and M. Klailova for their helpful comments. We thank M. McLennan in particular for extensive comments and discussions on the subject. This work was supported by a postdoctoral research grant to K.H. from Fundação para a Ciência e a Tecnologia, Portugal, and MEXT grant no. 20002001, JSPS-HOPE and JSPS-gCOE (A06, Biodiversity) to T.M.

References

- Ahlering, M. A., Millsaugh, J. J., Woods, R. J., Western, D. & Eggert, L. S. 2011. Elevated levels of stress hormones in crop-raiding male elephants. *Animal Conservation*, **14**, 124–130.
- Anderson, D. P., Nordheim, E. V., Boesch, C. & Moermond, T. C. 2002. Factors influencing fission–fusion grouping in chimpanzees in the Tai Forest, Cote d'Ivoire. In: *Chimpanzee Behavioural Diversity* (Ed. by C. Boesch, G. Hohmann & L. F. Marchant), pp. 90–101. Cambridge: Cambridge University Press.
- Anderson, D. P., Nordheim, E. V. & Boesch, C. 2006. Environmental factors influencing the seasonality of estrus in chimpanzees. *Primates*, **47**, 43–50.
- Asensio, N., Korstjens, A. H. & Aureli, F. 2009. Fissioning minimizes ranging costs in spider monkeys: a multiple-level approach. *Behavioral Ecology and Sociobiology*, **63**, 649–659.
- Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Di Fore, A., Dunbar, R. I. M. & Henzi, S. P., et al. 2008. Fission–fusion dynamics: new research frameworks. *Current Anthropology*, **48**, 627–654.
- Bates, L. A. & Byrne, R. W. 2009. Sex differences in the movement of free-ranging chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, **64**, 247–255.
- Bell, R. H. V. 1984. The man–animal interface: an assessment of crop damage and wildlife control. In: *Conservation and Wildlife Management in Africa* (Ed. by R. H. V. Bell & E. McShane-Caluzi), pp. 387–416. Washington DC: US Peace Corps Office of Training and Program Support.
- Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B. P. & Saltz, D. 2011. Integrating animal behavior and conservation biology: a conceptual framework. *Behavioral Ecology*, **22**, 236–239, doi:10.1093/beheco/arq224.
- Bettridge, C., Lehmann, J. & Dunbar, R. I. M. 2010. Trade-offs between time, predation risk and life history, and their implications for biogeography: a systems modelling approach with a primate case study. *Ecological Modelling*, **221**, 777–790.
- Boesch, C. 1996. Social grouping in Tai chimpanzees. In: *Great Ape Societies* (Ed. by W. McGrew, L. Marchant & T. Nishida), pp. 101–113. Cambridge: Cambridge University Press.
- Boesch, C. & Boesch-Achermann, H. 2000. *The Chimpanzees of the Tai Forest*. Oxford: Oxford University Press.
- Bradbury, J. W. & Vehrencamp, S. L. 1976. Social organization and foraging in emballonurid bats. *Behavioral Ecology and Sociobiology*, **1**, 337–381.
- Campbell-Smith, G., Campbell-Smith, M., Singleton, I. & Linkie, M. 2011. Apes in space: saving an imperilled orangutan population in Sumatra. *PLoS ONE*, **6**, e17210.
- Carvalho, S., Cunha, E., Sousa, C. & Matsuzawa, T. 2008. Chaines opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of Human Evolution*, **55**, 148–163.
- Chapman, C. A., Wrangham, R. W. & Chapman, L. J. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, **36**, 59–70.
- Cohen, J. 1992. A power primer. *Psychological Bulletin*, **112**, 155–159.
- Cowlshaw, G. 1999. Ecological and social determinants of spacing behaviour in desert baboon groups. *Behavioral Ecology and Sociobiology*, **45**, 67–77.
- Doran, D. 1997. Influence of seasonality on activity patterns, feeding behaviour, ranging and grouping patterns in Tai chimpanzees. *International Journal of Primatology*, **18**, 183–206.
- Dunbar, R. I. M., Korstjens, A. & Lehmann, J. 2009. Time as an ecological constraint. *Biological Reviews*, **84**, 413–429.
- Dunham, K. M., Ghiurghi, A., Cumbi, R. & Urbano, F. 2010. Human–wildlife conflict in Mozambique: a national perspective, with emphasis on wildlife attacks on humans. *Oryx*, **44**, 185–193.
- Forthman-Quick, D. L. 1986. Activity budgets and the consumption of human foods in two troops of baboons, *Papio anubis*, at Gilgil, Kenya. In: *Primate Ecology and Conservation* (Ed. by J. C. Else & P. C. Lee), pp. 221–228. Cambridge: Cambridge University Press.
- Forthman-Quick, D. L. & Demment, M. 1988. Dynamics of exploitation: differential energetic adaptations of two troops of baboons to recent human contact. In: *Ecology and Behavior of Food Enhanced Primate Groups* (Ed. by J. E. Fa & C. Southwick), pp. 25–51. New York: A.R. Liss.
- Fritz, S. A., Bininda-Emonds, O. R. P. & Purvis, A. 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters*, **12**, 538–549.
- Fuentes, A. & Hockings, K. J. 2010. The ethnoprimate approach in primatology. *American Journal of Primatology*, **72**, 841–847.
- Fuentes, A. & Wolfe, L. D. 2002. *Primates Face to Face: the Conservation Implications of Human–Nonhuman Primate Interconnections*. Cambridge: Cambridge University Press.
- Gillespie, T. R. & Chapman, C. A. 2001. Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological constraints model. *Behavioral Ecology and Sociobiology*, **50**, 329–338.
- Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, Massachusetts: Harvard University Press.
- Harris, R. A. 1970. Natural vs. purified diets in research with nonhuman primates. In: *Feeding and Nutrition of Nonhuman Primates* (Ed. by R. S. Harris), pp. 251–262. New York: Academic Press.
- Hashimoto, C., Furuichi, T. & Tashiro, Y. 2001. What factors affect the size of chimpanzee parties in the Kalinzu Forest, Uganda? Examination of fruit abundance and number of estrous females. *International Journal of Primatology*, **22**, 947–959.
- Hashimoto, C., Furuichi, T. & Tashiro, Y. 2003. How fruit abundance affects the chimpanzee party size: a comparison between four study sites. *Primates*, **44**, 77–81.
- Hoare, R. E. 1995. Options for the control of elephants in conflict with people. *Pachyderm*, **19**, 54–63.
- Hoare, R. E. 1999. Determinants of human–elephant conflict in a land-use mosaic. *Journal of Applied Ecology*, **36**, 689–700.
- Hockings, K. J. 2007. Human–chimpanzee coexistence at Bossou, the Republic of Guinea: a chimpanzee perspective. Ph.D. thesis, University of Stirling.
- Hockings, K. J. & Humle, T. 2009. *Best Practice Guidelines for the Prevention and Mitigation of Conflict between Humans and Great Apes*. Gland: IUCN/SSC Primate Specialist Group.
- Hockings, K. J. & Sousa, C. 2011. Human–chimpanzee sympatry and interactions in Cantanhez National Park, Guinea-Bissau: current research and future directions. *Primate Conservation*, number 26.
- Hockings, K. J., Anderson, J. R. & Matsuzawa, T. 2006. Road-crossing in chimpanzees: a risky business. *Current Biology*, **16**, 668–670.
- Hockings, K. J., Humle, T., Anderson, J. R., Biro, D., Sousa, C., Ohashi, G. & Matsuzawa, T. 2007. Chimpanzee share forbidden fruit. *PLoS ONE*, **2**, e886.
- Hockings, K. J., Anderson, J. R. & Matsuzawa, T. 2009. Use of wild and cultivated foods by chimpanzees at Bossou, Republic of Guinea: feeding dynamics in a human-influenced environment. *American Journal of Primatology*, **71**, 636–646.
- Hockings, K. J., Anderson, J. R. & Matsuzawa, T. 2010a. Flexible feeding on cultivated underground storage organs by rainforest-dwelling chimpanzees at Bossou, West Africa. *Journal of Human Evolution*, **58**, 227–233.
- Hockings, K. J., Yamakoshi, G., Kabasawa, A. & Matsuzawa, T. 2010b. Attacks on local persons by chimpanzees in Bossou, Republic of Guinea: long-term perspectives. *American Journal of Primatology*, **72**, 887–896.
- Isaac, N. J. B. & Cowlshaw, G. 2004. How species respond to multiple extinction threats. *Proceedings of the Royal Society B*, **271**, 1135–1141.
- Janson, C. H. & Goldsmith, M. L. 1995. Predicting group size in primates: foraging costs and predation risks. *Behavioral Ecology*, **6**, 326–336.
- Key, C. & Ross, C. 1999. Sex differences in energy expenditure in non-human primates. *Proceedings of the Royal Society B*, **266**, 2479–2485.
- Korstjens, A. H., Verhoeckx, I. L. & Dunbar, R. I. M. 2006. Time as a constraint on group size in spider monkeys. *Behavioral Ecology and Sociobiology*, **60**, 683–694.
- Korstjens, A. H., Lehmann, J. & Dunbar, R. I. M. 2010. Resting time as an ecological constraint on primate biogeography. *Animal Behaviour*, **79**, 361–374.
- Knott, C. D. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *International Journal of Primatology*, **19**, 1061–1079.
- Lee, P. C. 2010. Sharing space: can ethnoprimateology contribute to the survival of nonhuman primates in human-dominated globalized landscapes? *American Journal of Primatology*, **72**, 925–931.
- Lehmann, J. & Boesch, C. 2004. To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. *Behavioral Ecology and Sociobiology*, **56**, 207–216.
- Lehmann, J., Korstjens, A. H. & Dunbar, R. I. M. 2007. Fission–fusion social systems as a strategy for coping with ecological constraints: a primate case. *Evolutionary Ecology*, **21**, 613–634.
- Lehmann, J., Korstjens, A. H. & Dunbar, R. I. M. 2008. Time and distribution: a model of ape biogeography. *Ethology, Ecology and Evolution*, **20**, 337–359.
- McKinney, T. 2011. The effects of provisioning and crop-raiding on the diet and foraging activities of human-commensal white-faced capuchins (*Cebus capucinus*). *American Journal of Primatology*, **73**, 439–448.
- McLennan, M. R. 2008. Beleaguered chimpanzees in the agricultural district of Hoima, western Uganda. *Primate Conservation*, **23**, 45–54.
- McLennan, M. R. 2010. Chimpanzee ecology and interactions with people in an unprotected humandominated landscape at Bulindi, western Uganda. Ph.D. thesis, Oxford Brookes University.
- Martin, P. & Bateson, P. 1986. *Measuring Behaviour: an Introductory Guide*. Cambridge: Cambridge University Press.
- Matsuzawa, T., Humle, T. & Sugiyama, Y. 2011. *The Chimpanzees of Bossou and Nimba*. Tokyo: Springer.
- Mitani, J. C., Watts, D. & Lwanga, J. 2002. Ecological and social correlates of chimpanzee party size and composition. In: *Behavioral Diversity in Chimpanzees and Bonobos* (Ed. by C. Boesch, G. Hohmann & L. Marchant), pp. 102–111. Cambridge: Cambridge University Press.
- Morgan, B. J. 2009. *Sacoglottis gabonensis*: a keystone fruit for forest elephants in the Réserve de Faune du Petit Loango, Gabon. *African Journal of Ecology*, **47**, 154–163.

- Naughton-Treves, L. & Treves, A.** 2005. Socio-ecological factors shaping local support for wildlife: crop-raiding by elephants and other wildlife in Africa. In: *People and Wildlife: Conflict or Coexistence?* (Ed. by R. Woodroffe, S. Thirgood & A. Rabinowitz), pp. 252–277. Cambridge: Cambridge University Press.
- Naughton-Treves, L., Treves, A., Chapman, C. & Wrangham, R.** 1998. Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, **35**, 596–606.
- Newton-Fisher, N. E., Reynolds, V. & Plumptre, A. J.** 2000. Food supply and chimpanzee (*Pan troglodytes schweinfurthii*) party size in the Budongo Forest, Uganda. *International Journal of Primatology*, **21**, 613–628.
- Nishida, T.** 1968. The social group of wild chimpanzees in the Mahale Mountains. *Primates*, **9**, 167–224.
- Nishida, T., Kano, T., Goodall, J., McGrew, W. C. & Nakamura, M.** 1999. Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science*, **107**, 141–188.
- Osborn, F. V.** 1998. The ecology of crop-raiding elephants in Zimbabwe. Ph.D. thesis, University of Cambridge.
- Osborn, F. V.** 2004. Seasonal variation of feeding patterns and food selection by crop-raiding elephants in Zimbabwe. *African Journal of Ecology*, **42**, 322–327.
- Osborn, F. V. & Hill, C. M.** 2005. Techniques to reduce crop loss to elephants and primates in Africa; the human and technical dimension. In: *People and Wildlife: Conflict or Coexistence?* (Ed. by R. Woodroffe, S. Thirgood & A. Rabinowitz), pp. 72–85. Cambridge: Cambridge University Press.
- Owens, I. P. F. & Bennett, P. M.** 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences, U.S.A.*, **97**, 12144–12148.
- Priston, N.** 2005. Crop-raiding by *Macaca ochreata brunnescens* in Sulawesi: reality, perceptions and outcomes for conservation. Ph.D. thesis, University of Cambridge.
- Pruetz, J. D.** 2006. Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In: *Feeding Ecology in Apes and Other Primates* (Ed. by G. Hohmann, M. Robbins & C. Boesch), pp. 326–364. Cambridge: Cambridge University Press.
- Purvis, A., Gittleman, J. L., Cowlshaw, G. & Mace, G. M.** 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society B*, **267**, 1947–1952.
- Reader, S. M. & MacDonald, K. N.** 2003. Environmental variability and primate behavioural flexibility. In: *Animal Innovation* (Ed. by S. M. Reader & K. N. Laland), pp. 83–116. Oxford: Oxford University Press.
- Reynolds, V.** 2005. *The Chimpanzees of the Budongo Forest: Ecology, Behaviour, and Conservation*. Oxford: Oxford University Press.
- Reynolds, V., Wallis, J. & Kyamanywa, R.** 2003. Fragments, sugar, and chimpanzees in Masindi District, Western Uganda. In: *Primates in Fragments: Ecology and Conservation* (Ed. by L. K. Marsh), pp. 309–320. New York: Kluwer Academic/Plenum.
- Robinson, J. G.** 1981. Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivittatus*. *Animal Behaviour*, **29**, 1036–1056.
- Saj, T. L., Sicotte, P. & Paterson, J. D.** 1999. Influence of human food consumption on the time budgets of vervets. *International Journal of Primatology*, **20**, 977–994.
- Saj, T. L., Teichroeb, J. A. & Sicotte, P.** 2005. The population status of the ursine colobus (*Colobus vellerosus*) at Boabeng-Fiema sacred grove, Ghana. In: *Commensalism and Conflict: Human-Primate Interface* (Ed. by J. D. Paterson & J. Wallis), pp. 350–375. Norman, Oklahoma: American Society of Primatologists.
- Sakura, O.** 1994. Factors affecting party size and composition of chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea. *International Journal of Primatology*, **15**, 167–181.
- Saunders, D. A., Hobbs, R. J. & Margules, C. R.** 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, **5**, 18–32.
- Shimada, M. K., Hayakawa, S., Fujita, S., Sugiyama, Y. & Saitou, N.** 2009. Skewed matrilineal genetic composition in a small wild chimpanzee community. *Primates*, **80**, 19–32.
- Sokal, R. R. & Rohlf, F. J.** 1995. *The Principles and Practice of Statistics in Biological Research*. 3rd edn. New York: W. H. Freeman.
- Sol, D.** 2003. Behavioural innovation: a neglected issue in the ecological and evolutionary literature? In: *Animal Innovation* (Ed. by S. M. Reader & K. N. Laland), pp. 63–82. Oxford: Oxford University Press.
- Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P. & Lefebvre, L.** 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences, U.S.A.*, **102**, 5460–5465.
- Stephens, D. W. & Krebs, J. R.** 1986. *Foraging Theory*. Princeton, New Jersey: Princeton University Press.
- Strum, S. C.** 1984. The pumphouse gang and the great crop raids. *Animal Kingdom*, **87**, 36–43.
- Strum, S. C.** 1994. Prospects for management of primate pests. *Revue d'Ecologie: La Terre et la Vie*, **49**, 295–306.
- Strum, S. C.** 2010. The development of primate raiding: implications for management and conservation. *International Journal of Primatology*, **31**, 133–156.
- Sugiyama, Y.** 2004. Demographic parameters and life history of chimpanzees at Bossou, Guinea. *American Journal of Physical Anthropology*, **124**, 154–165.
- Sugiyama, Y. & Koman, J.** 1979. Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates*, **20**, 323–339.
- Sukumar, R.** 1990. Ecology of the Asian elephant in southern India II: feeding habits and crop raiding patterns. *Journal of Tropical Ecology*, **6**, 33–53.
- Sukumar, R.** 1991. The management of large mammals in relation to male strategies and conflict with people. *Biological Conservation*, **55**, 93–102.
- Sukumar, R. & Gadgil, M.** 1988. Male–female differences in foraging on crops by Asian elephants. *Animal Behaviour*, **36**, 1233–1255.
- Symington, M. M.** 1988. Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). *Behaviour*, **105**, 117–134.
- Takemoto, H.** 2004. Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical forest. *American Journal of Physical Anthropology*, **124**, 81–92.
- Terborgh, J. & Janson, C. H.** 1986. The socioecology of primate groups. *Annual Review of Ecology, Evolution and Systematics*, **17**, 111–136.
- Thouless, C. R.** 1994. Conflict between humans and elephants in northern Kenya. *Oryx*, **28**, 119–127.
- Treves, A.** 2009. The human dimensions of conflicts with wildlife around protected areas. Human–wildlife conflicts around protected areas. In: *Wildlife and Society: The Science of Human Dimensions* (Ed. by M. Manfredo, J. J. Vaske, P. Brown, D. J. Decker & E. A. Duke), pp. 214–228. Washington DC: Island Press.
- Tutin, C. E. G., Ham, R. M., White, L. J. T. & Harrison, M. J. S.** 1997. The primate community of the Lope Reserve, Gabon: diets, responses to fruit scarcity and effects on biomass. *American Journal of Primatology*, **42**, 1–24.
- Tweheyo, M. & Lye, K. A.** 2005. Patterns of frugivory of the Budongo Forest chimpanzees, Uganda. *African Journal of Ecology*, **43**, 282–290.
- Wilson, M. L., Hauser, M. D. & Wrangham, R. W.** 2007. Chimpanzees (*Pan troglodytes*) modify grouping and vocal behaviour in response to location-specific risk. *Behaviour*, **144**, 1621–1653.
- Woodroffe, R., Thirgood, S. & Rabinowitz, A.** 2005. *People and Wildlife: Conflict or Coexistence?* Cambridge: Cambridge University Press.
- Wrangham, R. W.** 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (Ed. by T. H. Clutton-Brock), pp. 504–538. London: Academic Press.
- Wrangham, R. W.** 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: *Male Primates* (Ed. by P. Kappeler), pp. 248–258. Cambridge: Cambridge University Press.
- Wrangham, R. W., Conklin, N. L., Chapman, C. A. & Hunt, K. A.** 1991. The significance of fibrous foods for the Kibale forest chimpanzees. *Philosophical Transactions of the Royal Society B*, **334**, 171–178.
- Yamakoshi, G.** 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. *American Journal of Physical Anthropology*, **106**, 283–295.
- Yamakoshi, G.** 2011. The 'prehistory' before 1976: looking back on three decades of research on Bossou chimpanzees. In: *The Chimpanzees of Bossou and Nimba* (Ed. by T. Matsuzawa, T. Humle & Y. Sugiyama), pp. 35–44. Tokyo: Springer.