Risk-prone hunting by chimpanzees (*Pan troglodytes schweinfurthii*) increases during periods of high diet quality

Ian C. Gilby · Richard W. Wrangham

Abstract Most studies suggest that during times of nutritional stress, an animal faced with two foraging choices should follow a risk-prone strategy, choosing the option with highest payoff variance. This "scarcity/risk" hypothesis was developed to account for the foraging patterns of small animals with high metabolic rates susceptible to the threat of starvation. In this paper, we propose that animals should also be risk-prone when their diet quality is particularly high, far exceeding that which is needed to survive. Under these circumstances, the costs of experiencing a low or negative payoff can easily be recouped. We suggest that large-bodied omnivores are most likely to adopt this "abundance/risk" strategy. We investigate this question among wild chimpanzees (*Pan troglodytes*) that choose between a risk-averse strategy of feeding on plant material and a risk-prone strategy of hunting red colobus monkeys. Using 14 years of data on the Kanyawara chimpanzees of Kibale National Park, Uganda, we find strong evidence that chimpanzees follow the "abundance/risk" strategy. Both hunting rate (hunts/100 observation hours) and the probability of hunting upon encountering red colobus monkeys were positively correlated with seasonal consumption of ripe drupe fruits, a class of preferred food associated with elevated reproductive performance by females. Critically, these results remained statistically significant after controlling for the potentially confounding effects of male chimpanzee party size and the presence of sexually receptive females. These findings suggest that the relationship between risk-sensitive foraging and diet quality depends upon the daily probability of starvation, the number of alternative foraging strategies, and the degree to which diet quality satisfies an animal's nutritional requirements.

Keywords Chimpanzee · Hunting · Risk-sensitive foraging · Diet quality

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Introduction

Studies in several taxa show that animals are sensitive to the risk (variance) associated with foraging choices and that a forager's risk-proneness may be based on its nutritional state (reviewed in Kacelnik and Bateson 1996; Bateson and Kacelnik 1998; Bateson 2002). Current theory predicts that when faced with a choice between strategies with equal expected payoffs, an animal should be "risk-prone" (choosing the option with higher payoff variance) when its nutritional requirement is greater than the expected payoff (Stephens 1981). Choosing a risk-prone strategy improves the odds of obtaining an above-average payoff, thus, increasing the chances that the animal will obtain enough food to survive. By contrast, if its nutritional requirement is less than the average expected payoff, the animal should follow a "risk-averse" strategy, choosing the low-variance option. Thus, animals subject to a short-term threat of starvation are expected to take more foraging risks when food is scarce.

Stephens' (1981) theory rests on the assumption that if a certain level of food intake is not achieved by the end of the day, the animal will die. Animals should therefore be more likely to take risks during periods when diet quality is extremely poor. We refer to this concept as the "scarcity/risk" hypothesis. Several studies of small animals support
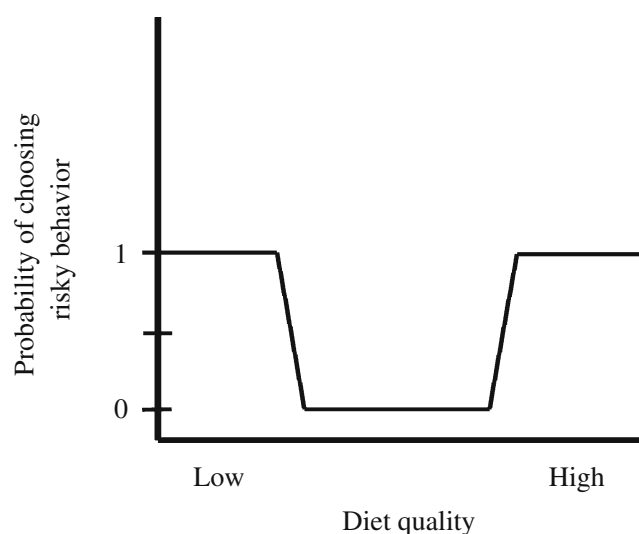
this idea (e.g., yellow-eyed juncos, *Junco phaeonotus*: Caraco et al. 1990; bumblebees, *Bombus occidentalis*: Cartar and Dill 1990; 15-spined stickleback, *Spinachia spinachia*: Croy and Hughes 1991; reviewed in Kacelnik and Bateson 1996). While we do not dispute the scarcity/risk hypothesis, we suggest that it does not exhaust the possibilities. In particular, larger bodied species never experience high daily risks of starvation, although they are exposed to substantial variation in food supply. For some, there are occasional periods when food is superabundant (e.g., coyotes, *Canis latrans*, bobcats, *Lynx lynx* (Odonoghue et al. 1997), and lions, *Panthera leo* (Kissui and Packer 2004). We propose that such animals should be risk-prone during these periods of food abundance. This is because a negative payoff is less costly when an animal can easily obtain calories elsewhere or rely on its energy stores. We refer to this concept as the "abundance/risk" hypothesis. The abundance/risk and scarcity/risk hypotheses are not mutually exclusive. Instead, rather than focus on the starvation threshold, the abundance/risk hypothesis makes predictions about foraging decisions at the other end of the diet quality spectrum. Together, the two hypotheses predict that the probability of exhibiting risk-prone foraging behavior follows a U-shaped function, peaking when diet quality is either very low or very high (Fig. 1). They suggest that an animal should be risk-averse when diet quality is at an intermediate level, that is, when it is not at risk of starvation, but cannot afford the costs associated with choosing a food item with a highly variable payoff.

Chimpanzees (*Pan troglodytes*) offer a test of the abundance/risk hypothesis because they forage on two distinct food types which show clear differences in pay-off variance. Their low-variance foods are plant items such as

ripe fruit (typically more than 50% of feeding time), leaves, and stems. A chimpanzee that encounters a feeding patch containing these items faces a minimal risk of foraging failure after a decision to enter the food patch and eat. Their high-variance foods, by contrast, are mammalian prey (Wrangham 1977; Nishida et al. 1979; Goodall 1986). Chimpanzees prey most frequently upon red colobus monkeys, *Procolobus spp.* (Uehara 1997; Mitani and Watts 2001). Meat of these and other species is clearly prized by chimpanzees (Stanford 1998) presumably because of its nutritional value (Milton 2003). However, it is also risky to acquire because many hunts fail completely. The failure rate is roughly 50% at Taï National Park, Côte d'Ivoire (Boesch and Boesch-Achermann 2000) and Gombe National Park, Tanzania (Gilby et al. 2006) and 16% at Ngogo, Kibale National Park, Uganda (Mitani and Watts 2001). Hunts of red colobus involve frequent rapid climbing, indicating high-energy expenditure (Pontzer and Wrangham 2004). They average 18.9 min in duration and can last for as long as 120 min (Goodall 1986; Boesch and Boesch 1989). Thus, meat is a high-risk food item compared to plant matter. Note that while chimpanzee hunters may face considerable risk of being wounded (Busse 1977; Boesch and Boesch 1989; Stanford 1995), we are adhering here to the traditional variance-based definition of risk, i.e., failure to obtain a prey item.

Chimpanzees have a fission–fusion social system in which members of a community form temporary parties of changing size and composition (Nishida 1968; Wrangham and Smuts 1980; Goodall 1986). The availability of ripe fruit in chimpanzee habitat varies considerably over time, resulting in alternating but unpredictable periods of nutrient shortfall or abundance (Chapman et al. 1995; Wrangham et al. 1998). Therefore, according to the abundance/risk hypothesis, chimpanzees should increase their hunting of red colobus monkeys (i.e., be more risk-prone) when overall diet quality is high.

Preliminary data on chimpanzee hunting behavior provide conflicting results with respect to these expectations. Both at Ngogo and Mahale Mountains National Park, Tanzania, hunting frequency was high during periods when ripe fruit was plentiful (Mahale: Nishida et al. 1979; Takahata et al. 1984; Ngogo: Mitani and Watts 2001; Watts and Mitani 2002a, b). This appears to support the abundance/risk hypothesis. In contrast, chimpanzees at Gombe hunted more frequently during the dry season (Stanford et al. 1994; Gilby 2004) when body masses tend to be low (Pusey et al. 2005), supporting the scarcity/risk hypothesis. However, to test whether fruit availability had a direct effect on hunting frequency, two important confounding variables must be controlled for.

First, hunting probability increases with chimpanzee party size (Stanford et al. 1994; Mitani and Watts 2001;

Fig. 1 Modified risk-sensitive foraging model. Animals are expected to adopt a risk-prone foraging strategy when diet quality is either very poor or far exceeds their basic nutritional requirements

Watts and Mitani 2002a; Gilby et al. 2006), which is positively correlated with fruit availability (Goodall 1986; Chapman et al. 1994; Matsumoto-Oda et al. 1998; Wrangham 2000; Anderson et al. 2002; Mitani et al. 2002). Second, the presence of sexually receptive females may affect hunting by adult males. Female chimpanzees advertise their receptivity with a conspicuous ano-genital swelling (Goodall 1986; Wallis 1997), and the number of such "swollen" females in a chimpanzee party is correlated with fruit abundance (Wrangham 2002) and party size (Stanford et al. 1994; Matsumoto-Oda 1999; Anderson et al. 2002; Mitani et al. 2002; Emery Thompson and Wrangham 2006). Adult males may seek meat to trade for mating, and therefore, would be more likely to hunt if swollen females were present ("meat-for-sex"; Stanford et al. 1994). Alternatively, males may forego hunting opportunities to mate-guard ("meat-or-sex"; Gilby et al. 2006).

Therefore, to demonstrate a direct effect of fruit availability (and/or diet quality) on hunting probability, one must statistically control for party size and the presence of swollen females. When data from Ngogo and Gombe were analyzed in this way, hunting probability was no longer associated with fruit availability (Ngogo: Mitani and Watts 2005) or diet quality (Gombe: Gilby et al. 2006), indicating an indirect relationship between diet quality and risk-proneness.

In this study, we use 14 years of data from the Kanyawara chimpanzee community in Kibale National Park, Uganda to test whether seasonal variation in hunting frequency can be explained by the abundance/risk hypothesis. We use multivariate statistics to control for the effects of adult male party size and the presence of swollen females.

Materials and methods

Study site and long-term data collection

Systematic data collection on the Kanyawara community has been continuous since 1988. The chimpanzees were habituated to the presence of humans without provisioning, and all adult males were fully habituated by January 1990. The size and composition of the Kanyawara community has remained relatively stable, averaging about 40–50 individuals, with 9–12 adult males and 12–15 adult females occupying an area of approximately 32 km^2 (Wilson 2001). Each day, two or more Ugandan field assistants, often accompanied by one or more researchers, locate a party of chimpanzees by utilizing nesting information from the previous day, listening for vocalizations, or checking recent feeding sites. The team follows the party for as long as possible, usually until the animals build their night nests. If

the party splits, observers follow the larger subgroup. At 15-min intervals, the observers use scan sampling (Altmann 1974) to record party composition and feeding behavior. If at least one chimpanzee is feeding, they record the species and part (ripe fruit, leaves, etc.) being consumed. Since January 1996, they have recorded the presence of other primate species within 100 m. They also record the occurrence of all major events, including hunting, in narrative notes. All data, along with detailed demographic information on each chimpanzee, are digitized and stored in a relational database in the Department of Anthropology at Harvard University.

Diet quality

"Preferred" foods are those eaten in proportion to their availability, i.e., showing a positive correlation between feeding time and a phenological index (Wrangham et al. 1991). By this definition, the Kanyawara chimpanzees preferentially consume ripe arboreal drupes, or "non-fig fruits" (NFF), when available (Wrangham et al. 1996; Emery Thompson 2005). This indicates that NFF are high-quality food items. Indeed, at Kanyawara, intake of lipids, simple sugars, and nonstructural carbohydrates was positively correlated with ripe fruit abundance (Conklin-Brittain et al. 1998), which was driven by variation in NFF (Wrangham et al. 1996). The benefits of elevated NFF intake are striking. NFF consumption at Kanyawara was highly positively correlated with several energetically expensive factors associated with increased fitness including ovarian function, likelihood of sexual swelling (Emery Thompson 2005), and probability of conception (Sherry 2002; Emery Thompson 2005). Thus, we treat NFF consumption as a powerful measure of diet quality at Kanyawara.

We therefore index temporal variation in diet quality by the chimpanzees' exploitation of NFF. We counted the number of 15-min scans per month that chimpanzees were observed feeding. We then calculated NFF consumption, which we defined as the percentage of feeding scans that NFFs accounted for. However, because some fruit crops last for many weeks, adjacent months often have similar fruiting patterns and are not necessarily statistically independent. Therefore, to reduce pseudoreplication, we used the monthly NFF consumption values to identify "NFF" and "Other Food" seasons. If chimpanzees spent more than 40% of their feeding time on NFF in two or more consecutive months, we lumped these months into a single "NFF" season. We classified adjacent months with less than 40% NFF consumption as "Other Food" seasons. We then calculated a single NFF consumption value for each season (of both types) by averaging the NFF consumption values of its component months. We exclud-

ed seasons with fewer than 150 observation hours from all subsequent analyses.

In short, we used the percentage of diet comprised of NFF to identify dietary seasons. To reduce pseudoreplication, we used these seasons (instead of months) as sampling units for all subsequent analyses. In the remainder of the paper, 'NFF consumption' refers to the percentage of feeding scans during a given season (of either type, NFF or Other Food) that NFF accounted for.

Male party size and observation time

To calculate the total number of observation hours per season, we summed the number of 15-min scans that chimpanzees were observed and divided by four. We classified each chimpanzee party according to the number of adult and adolescent (greater than 10 years old) males that were present. We then counted the number of 15-min scans per season that parties of each size were observed. We divided this value by four to obtain the number of observation hours for each.

Encounters and hunts

We identified all instances when red colobus monkeys were present within 100 m of the chimpanzee party. These data were only available between January 1996 and December 2003. For each of these "encounters", we recorded the date and time, how many swollen females, adult and adolescent male chimpanzees were present, whether or not at least one chimpanzee hunted, and if at least one monkey was killed.

We defined hunting as "climbing to attack or chase one or more monkeys". For the period between January 1990 and December 2003, we identified all hunts (successful and unsuccessful) of red colobus monkeys from the narrative notes. Not all encounters with red colobus monkeys were recorded between January 1990 and December 1995.

Statistical analysis

We conducted all statistical analyses in SAS 9.1 (SAS Institute, Cary, NC, USA). For all multiple regressions, we began with the fully saturated model and removed insignificant interaction terms using manual stepwise backwards elimination. We used $\alpha=0.05$ as our criterion for significance; however, in practice, the p values of terms we removed were much greater than 0.05. For clarity, the details of each statistical test are included in "Results".

Results

Seasons

Our classification of months into NFF and Other Food "seasons", as described above, generated 46 seasons during the 168-month period from January 1990 to December 2003 (Fig. 2). Seasons ranged in length from 1 to 10 months, and seasonal NFF consumption ranged from 3.3 to 80.4% (mean±SD=42.4±26.1). There were 27 NFF seasons (during which, NFF consumption in two or more consecutive months was greater than 40%), and of these, 19

Fig. 2 Seasonal NFF consumption, January 1990–December 2003. Adjacent months in which >40% of feeding time was spent consuming NFF were lumped into a single "NFF" season, as described in the text. Seven periods with insufficient observation time (<150 h) were excluded from the analysis and are blank in the figure. There was considerable variation in NFF consumption over the course of the study
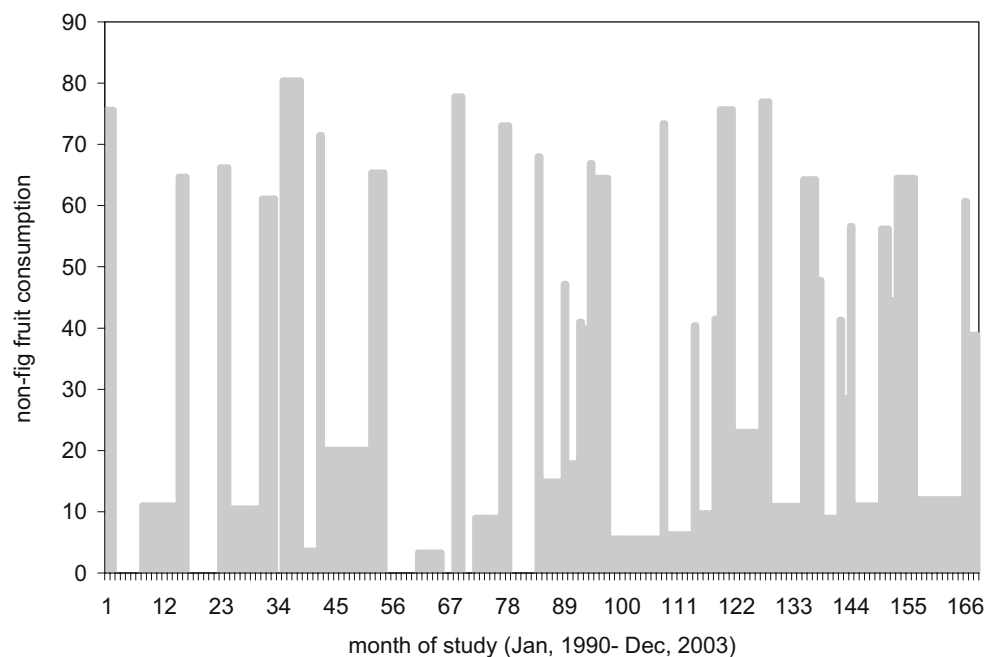
had a dominant fruit species, which accounted for more than 50% of NFF feeding time. These were *Mimusops bagshawei, Pseudospondias microcarpa*, and *Uvariopsis congensis*, which accounted for ten, three, and six seasons, respectively. The remaining eight NFF seasons did not have a dominant species. There were 19 Other Food seasons (during which, NFF consumption in component months was less than 40%).

Encounters and hunts

We recorded a total of 152 hunts of red colobus monkeys between January 1990 and December 2003. Seventy-four (49%) resulted in the capture of at least one monkey. The maximum killed in a single hunt were seven. There were a total of 790 encounters with red colobus monkeys between January 1996 and December 2003. A hunt occurred in 106 (13.4%) of these encounters. If we considered only those encounters at which there was at least one adult or adolescent male, the likelihood of hunting was 17.0% (104/610).

Hunting rate

We assessed the influence of seasonal diet quality on hunting rate by considering the frequency of hunting per 100 h of observation as a function of NFF consumption. Hunting rate (hunts/100 h) was significantly positively correlated with seasonal NFF consumption (linear regression: $F_{1,45}=12.20$, $R^2=0.22$, $P=0.001$). However, this may have been due to the fact that the mean number of males per party increased with NFF consumption (linear regression: $F_{1,45}=17.98$, $R^2=0.29$, $P=0.0001$), and hunting rate was also positively correlated with mean male party size (linear regression: $F_{1,10}=15.58$, $R^2=0.63$, $P=0.003$).

Therefore, we needed to consider the effect of male party size in our analysis. Small sample sizes prevented us from obtaining hunting rates for each party size in each individual season. Therefore, we could not use NFF consumption as a continuous variable as we had in the previous analyses. Instead, we summed the number of hunts by parties of each size (1–12 males) across all NFF seasons and divided this value by the number of minutes that parties of each size were observed during NFF seasons. We repeated this procedure for Other Food seasons (Table 1).

Then, we used an exact Wilcoxon signed ranks test to compare hunting rates in NFF vs Other Food seasons at each male party size, excluding party size/season combinations with fewer than 150 observation hours. This analysis demonstrated that at a given male party size, the hunting rate (hunts/100 h) was significantly higher in NFF seasons than in Other Food seasons ($N=9$, $S=105$, $P=0.04$, Fig. 3). Examination of the plot indicates that the positive effect of

Table 1 Hunting rates vs party size and season

| Males	Season					
	NFF			Other Food		
	Hunts	Hours	Hunts/ 100 h	Hunts	Hours	Hunts/ 100 h
1	0	1,088	0.00			
2	0	735	0.00	1	1,458	0.07
3	1	677	0.15	2	993	0.20
4	6	702	0.85			
5	4	662	0.60	2	748	0.27
6	15	680	2.21	8	874	0.92
7	13	900	1.44	9	929	0.97
8	17	820	2.07	6	708	0.85
9	15	875	1.71	5	775	0.65
10	12	737	1.63	3	574	0.52
11	7	485	1.44	1	255	0.39

At most party sizes with sufficient data (>150 observation hours/party size/season type), hunting rate (hunts/100 h) was higher in NFF seasons than Other Food seasons.

NFF on hunting rate was highest for parties with at least five males.

Hunting probability

One possible explanation for the increased hunting rate when more preferred fruit was eaten is that chimpanzee parties tend to be larger when food is abundant (Goodall 1986; Chapman et al. 1994; Matsumoto-Oda et al. 1998; Wrangham 2000; Anderson et al. 2002; Mitani et al. 2002), and larger parties travel greater distances than small parties (Chapman et al. 1994). Greater daily path length might lead to more encounters with colobus monkeys, and therefore, more hunts (Gilby 2004). Consequently, we performed another set of analyses using each red colobus encounter as our sampling unit. Logistic regression revealed that when chimpanzees encountered red colobus monkeys, the probability that a hunt occurred (Yes/No) increased with NFF consumption (logistic regression: $\chi_1^2 = 22.7$, $P<0.0001$). However, as before, the probability of hunting upon encountering red colobus monkeys also increased with male party size (logistic regression: $\chi_1^2 = 22.7$, $P<0.0001$). Additionally, the probability of a hunt occurring was significantly higher if at least one swollen female was present in the party (logistic regression: $\chi_1^2 = 8.49$, $P= 0.004$). When we used multiple logistic regression to control for both male party size and the presence of at least one swollen female, there was still a statistically significant positive association between hunting probability and NFF consumption ($\chi_1^2 = 6.12$, $P=0.01$, Table 2). NFF and male party size were not highly correlated (Pearson's $r= 0.25$); thus, collinearity was not a concern.

Fig. 3 Hunting rate vs chimpanzee males per party and NFF consumption. At a given male party size, hunting frequency was significantly higher in NFF seasons (*filled square*) than during Other Food seasons (*circle*). The magnitude of this effect increased with male party size. *Lines* are for reference only. Data were analyzed using a nonparametric Wilcoxon signed rank test
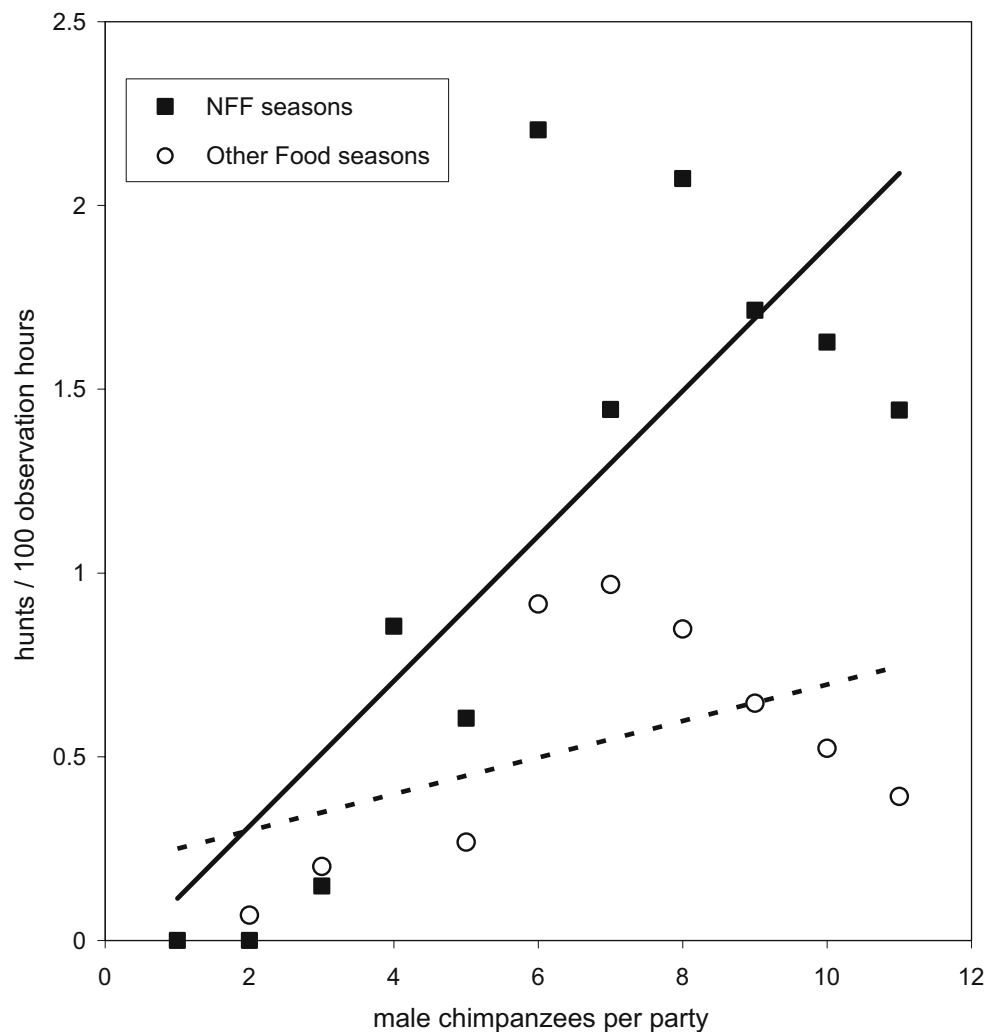
Additionally, another multiple logistic regression demonstrated a significant association between the dominant fruit species consumed during a given season and hunting probability ($\chi^2_4 = 34.9$, $P<0.0001$) even after controlling for male party size and the presence of at least one swollen female ($\chi^2_4 = 18.05$, $P=0.001$). Compared to Other Food seasons, encounters were significantly more likely to lead to hunts in seasons where the major food was *P. microcarpa* ($\chi^2_1 = 14.9$, $P=0.0001$, Fig. 4) or *M. bagshawei* ($\chi^2_1 = 4.1$, $P=0.04$, Fig. 4).

Table 2 Output from a multiple logistic regression of hunting probability vs the number of adult males and swollen females in the party and seasonal NFF consumption

Variable	df	Odds ratio	χ^2	p
Adult males	1	1.36	62.02	<0.0001
NFF consumption	1	1.01	6.12	0.0134
Swollen females	1	0.79	1.02	0.3136

After controlling for the significant positive effect of adult males, there was still a significant positive effect of seasonal NFF consumption on hunting probability.

Kills

There was a positive association between the number of males present at a hunt and the probability that a kill was made (logistic regression: $\chi^2_1 = 5.44$, $P=0.02$). However, there was no effect of NFF consumption on the probability that a hunt was successful ($\chi^2_1 = 0.03$, $P=0.87$) even after controlling for the number of males ($\chi^2_1 = 0.47$, $P=0.49$). Similarly, there was no effect of the dominant fruit species on the probability of success ($\chi^2_4 = 1.53$, $P=0.82$) even after controlling for the number of males ($\chi^2_4 = 0.67$, $P=0.95$).

Discussion

The Kanyawara chimpanzees were more likely to hunt red colobus monkeys during periods when diet quality was high, as measured by the proportion of feeding time spent eating non-fig fruits (NFF). Several lines of evidence indicate that NFF are a high-quality food source for these

Fig. 4 Probability of hunting upon encountering red colobus monkeys vs chimpanzee males per party and dominant fruit species. Logistic regression lines (with 95% confidence intervals) show that at a given male chimpanzee party size, a hunt was significantly more likely to occur during *Pseudospondias microcarpa* (*filled square*) and *Mimusops bagshawei* (*circle*) seasons than during Other Food seasons (*filled triangle*)
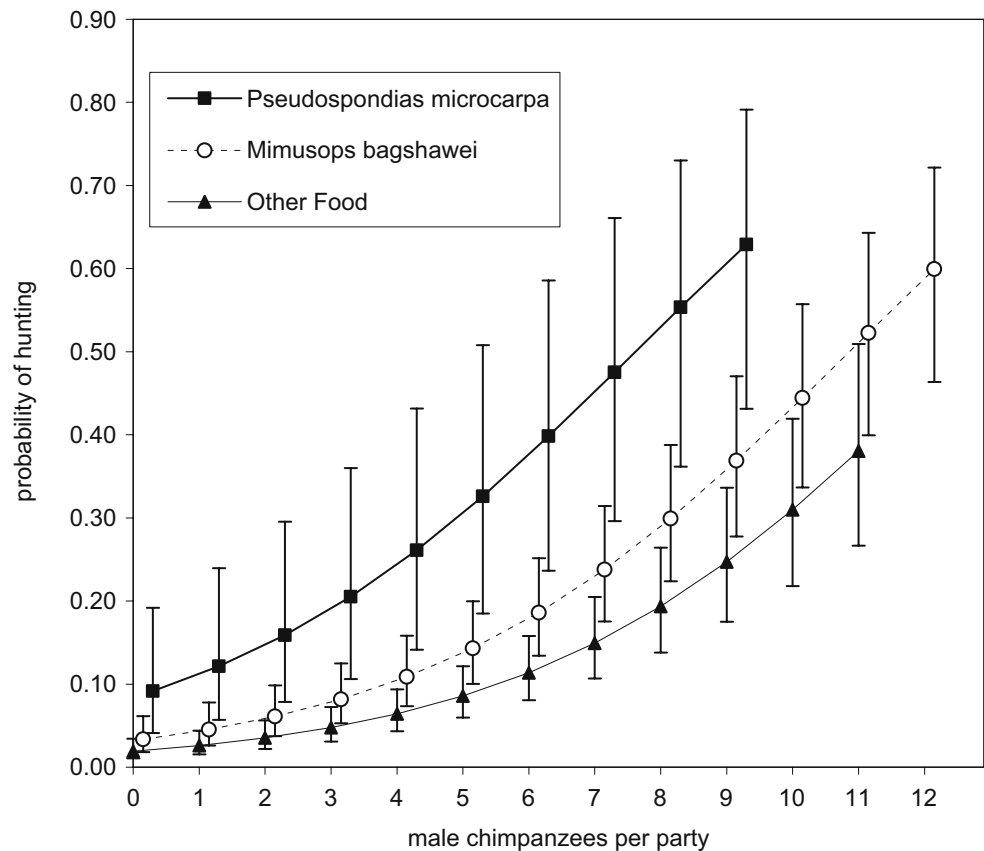
chimpanzees. They prefer to consume NFF when available (instead of figs, which are available year-round), and NFF consumption is positively correlated with estrogen production, sexual swelling (Emery Thompson 2005), and probability of conception (Sherry 2002; Emery Thompson 2005).

By statistically controlling for male chimpanzee party size and the presence of sexually receptive females, both of which are correlated with hunting frequency and NFF consumption, we showed that diet quality had a direct effect on hunting rate. At a given male party size, the hunting rate was higher in NFF seasons than in Other Food seasons. Hunting probability increased with NFF consumption whether or not sexually receptive females were present. Additionally, our analysis of the probability of hunting upon encountering red colobus monkeys eliminates the possibility that the observed increase in hunting rate during NFF seasons was due to more frequent encounters with potential prey during these periods.

These findings are also consistent with the 'nutrient surplus' hypothesis (Mitani and Watts 2001, 2005; Gilby et al. 2006) which states that chimpanzees may hunt more frequently when diet quality is high because they are more capable of compensating for the energetic costs of hunting at these times. This is subtly different from the abundance/risk hypothesis, which hinges specifically upon the costs of

failure. We frame our discussion in terms of risk-sensitivity to facilitate comparison across taxa.

Our results contrast with findings from Ngogo and Gombe where fruit availability had an indirect effect on hunting frequency through increases in party size (Ngogo: Mitani and Watts 2005; Gombe: Gilby et al. 2006). The reasons for this discrepancy are unclear. For example, it may be that chimpanzees at Kanyawara experience greater fluctuations in diet quality than at Gombe and Ngogo. Thus, Kanyawara chimpanzees might be more likely to approach the abundance/risk region of the U-shaped risk-sensitive foraging function (Fig. 1). However, such comparisons cannot be made without detailed data on net energy consumption. Alternatively, these discrepancies may also reflect methodological differences among sites. Mitani and Watts (2005) used an index of ripe fruit abundance, while Gilby et al. (2006) used a measure of diet quality based on consumption of fruit, leaves, and pith. Future comparative studies should use methods and indices that are as similar as possible.

In theory, it is possible that chimpanzees hunt in response to shortages of specific macronutrients rather than energy in general. Protein is the most likely candidate, but Conklin-Brittain et al. (1998) demonstrated that protein intake varies little for the Kanyawara chimpanzees and is always high in relation to nutritional needs. Also, the

individuals most at risk of specific macronutrient shortage would presumably be low-ranking females and young. However, meat is eaten mainly by adult males, whereas some females and young eat little or no meat. Thus, it is unlikely that hunting patterns are driven by specific macronutrient deficiencies as opposed to an appetite for energetically valuable food.

We interpret our results in terms of foraging risk. The traditional risk-sensitivity foraging model focuses upon the starvation threshold. It predicts that animals will be risk-prone when they face starvation, but will be risk-averse when their diet quality is adequate. We suggest a modification to this model, proposing that animals can afford to be risk-prone during periods when their diet quality greatly exceeds that which is simply required for survival. Our conclusions clearly support this 'abundance/ risk' hypothesis, for the Kanyawara chimpanzees were more likely to choose to hunt (a high-risk strategy) during periods when their diet quality was particularly high.

The width and steepness of the resulting U-shaped risk-proneness curve (Fig. 1) are likely to vary by species. Small-bodied animals with high metabolic rates are likely to experience an abrupt switch to risk-proneness at the starvation threshold. In contrast, chimpanzees, for which no deaths from starvation have been documented, may rarely (if ever) adopt a risk-prone foraging strategy when diet quality is low. When food is scarce, the low-risk strategy (foraging on plant material) may be a safe option for chimpanzees.

Our results thus suggest that the relationship between risk-sensitive foraging and diet quality depends upon such variables as the daily probability of starvation, the probability of failure, the number of alternative foraging strategies, and the degree to which diet quality satisfies an animal's nutritional requirements. Studies of other omnivorous mammals may be able to test the importance of such variables, but few relevant data exist. In one study of white-faced capuchins, *Cebus capuchinus*, the group with the richest habitat had the highest hunting rate (Rose 1997). However, in earlier studies of the same capuchin population, hunting frequency was highest in groups with the most marginal habitat and/or reduced food abundance (Chapman and Fedigan 1990; Fedigan 1990). A complicating factor in evaluating such results is that predation may depend upon prey availability. For example, brown bears (*Ursus arctos*) consume salmon (*Oncorhynchus* ssp) in direct proportion to salmon population density (Nevin and Gilbert 2005).

Ecological influences on the frequency of risk-prone hunting are therefore sensitive to cross-specific differences in behavior. We suggest that animals could theoretically be risk-prone when food is either very scarce or superabundant. The traditional view of risk-sensitive foraging is most relevant to small-bodied, high-metabolism species that face a real risk of starvation. In contrast, large-bodied omnivores are expected to be generally risk-averse, but may adopt a risk-prone foraging strategy when their diet quality is particularly high and they can easily recoup the costs of failure.

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