The relationship between food calling and agonistic behaviour in wild chimpanzees

Géraldine Ischer [1], Klaus Zuberbühler [1, 2] and Pawel Fedurek [3]

[1] University of Neuchâtel, Department of Comparative Cognition, Neuchâtel, Switzerland

[2] School of Psychology and Neuroscience, University of St Andrews, St Andrews, UK

[3] Division of Psychology, Faculty of Natural Sciences, University of Stirling, Stirling, UK

Corresponding author: Pawel Fedurek, University of Stirling, Division of Psychology, FK9 4LA, Stirling, Scotland (UK). Tel: +44 (0)1786 467844; email: pawel.fedurek@stir.ac.uk

Abstract

A number of social animals produce food-associated calls, which have been interpreted as informative and referential about the quality or quantity of food accessed by the caller. In chimpanzees, however, some behavioural patterns have remained unexplained by this model, suggesting that food-associated calls have a more generalized social function beyond attracting others to food, such as promoting tolerance between co-feeding individuals. In this study, we investigated how wild chimpanzees (*Pan troglodytes schweinfurthii*) of Budongo Forest, Uganda, use food associated-calls in situations when social tolerance is low, i.e., during agonistic interactions. We found a positive relationship between food calling and agonistic behaviours during a feeding event, independent of the number of males on the feeding patch. Moreover, food calling followed rather than preceded agonistic interactions, suggesting that aggression can trigger food call production. These results support the view that chimpanzee food-associated calls can act as social tools mediating competitive or aggressive interactions.

Key words: Aggression; Chimpanzee; Conflict; Food-associated calls

1. Introduction

Vocal communication sometimes allows receivers to infer something about the event experienced by the caller, effectively establishing a referential relationship between call type and external event (‘functional reference’) (Marler et al. 1992; Macedonia & Evans 1993; Bradbury & Vehrencamp 1998; Stegmann 2013). The functional reference hypothesis has originally been proposed for alarm call behaviour but more recently also to explain vocal behaviour in food-related events (Townsend & Manser 2013) with many birds and mammals producing distinct vocal signals in feeding contexts (Clay et al. 2012).

Chimpanzees (*Pan troglodytes*) are amongst the species that produce such food-associated calls, the 'rough grunts' (Goodall 1986; Slocombe & Zuberbühler 2005). In one experimental study, a captive chimpanzee responded to playbacks of food-associated calls as if they informed him about the location and type of food (Slocombe & Zuberbühler 2005). In the wild, chimpanzees also produce food-associated calls whose structure depends on food type and abundance (Slocombe & Zuberbühler 2006; Fedurek & Slocombe 2013; Kalan et al. 2015), which has led to the idea that these calls inform others about the presence of food.

However, some other studies have suggested that, in great apes, the 'functional reference' hypothesis of food-associated calls does not explain the entire range of behavioural patterns. In both chimpanzees and gorillas (*Gorilla gorilla*) food-associated calls appear to coordinate feeding decisions between co-feeders and to facilitate cohesion (Fedurek & Slocombe 2013; Luef et al. 2016). This suggests a social function of these calls beyond attracting others to food. Moreover, in chimpanzees, food-associated calls are produced more often in the presence of affiliated individuals ('friends'), suggesting a role in social bonding (Slocombe et al. 2010; Fedurek & Slocombe 2013). Similarly, arrival of high-ranking individuals can trigger food calling in lower ranking chimpanzees, even if they had been feeding for a while (Schel et al. 2013). Possible explanations for these patterns are that chimpanzee food-associated calls function to attract valuable social partners, such as friends and dominant individuals, and/or to coordinate feeding activities with them (Schel et al. 2013; Fedurek & Slocombe 2013).

Another, not incompatible, view is that food-associated calls promote co-feeding events, which are prone to aggressive escalation (Isabirye-Basuta, 1988; Wrangham and White, 1988). In chimpanzees, dominance relationships, especially among males, are mainly established by aggression and intimidation (Muller & Mitani 2005). Since in this species aggressive interactions and food calling commonly co-occur during feeding, they might be related. To date, however, there have been no systematic studies looking at the relationship between food calling and agonistic behaviour in chimpanzees. To address this, we examined whether the production of food-associated calls and the duration of calling were related to feeding events that were accompanied by agonistic interactions. We also investigated whether food calling followed rather than preceded agonistic interactions, which should be expected if food-associated calls are produced as a response to aggression rather than vice versa.

2. Methods

2.1 Study site and subjects

The study was conducted with members of the Sonso community in Budongo Forest, Uganda, between the 19 August 2017 and 23 January 2018. During the time of the study, the community comprised about 75 individuals. The community has been studied since 1990 and is fully habituated to human presence (Reynolds 2005). Study subjects were all individuals of the community, including 10 adult (15>years old; (Goodall 1986)) and 3 late adolescent (13-15 years old) males, as well as 24 adult (16>years old) and 4 late adolescent (11-14 years old) females.

2.2 Ethical note

Data collection was entirely observational and non-invasive. The study was approved by the Uganda Wildlife Authority and the Uganda National Council for Science and Technology.

2.3 Data collection

2.3.1 Feeding behaviour

A randomly selected adult or late adolescent male was followed between 07:00 and 16:30 local time (N=62 focal follows of N=13 males). Once the subject entered a food patch, we recorded the duration of food-calling coming from the focal individual's food patch, regardless of the identity or number of individuals producing the calls (e.g. Vogel & Janson 2007). We further recorded any occurrence of agonistic or aggressive interactions exhibited by any party member (Vogel & Janson 2007).

A feeding event started when the subject entered a food patch and ended when it exited a food patch. Food patches were defined as a tree or shrub used as a food source (Fedurek & Slocombe 2013). During each feeding event, we noted the type of food consumed by the feeding animals, which consisted of fruits, leaves, flowers, seeds or dead wood. Only complete feeding events (N=231, mean duration=27.47 min, minimum duration=0.23 min, maximum duration=155.67 min), i.e., where the subject was seen entering and leaving a food patch, were incorporated in the analysis.

We recorded the presence of all adult and late adolescent males and females in the feeding patch, as well as the time and identities of individuals joining or leaving the food patch.

2.3.2 Vocal behaviour

Chimpanzee food-associated calls are acoustically distinct and easily recognisable. They consist of sequences of either loud, high-pitched vocalizations with clear harmonic structures (‘food barks’ or ‘squeaks’) or of soft, low-pitched, noisy calls (‘rough grunts’) (Goodall 1986; Fedurek & Slocombe 2013). Chimpanzees not only call when discovering a new food source but they often also resume calling during ongoing feeding. A digital watch and a notepad were used to record food calling durations. The start time of food calling was noted once food-associated calls were heard from the feeding patch, while end time when no food-associated calls were heard for a period of 5s. We then considered subsequent food calling bouts as distinct if they were separated by at least one minute of non-food calling (i.e. no individual at the feeding patch food called during that period). Total food calling duration (in seconds) was defined as the sum of durations of all food calling bouts during a feeding event (given by the entire group on a feeding patch).

2.3.3 Agonistic behaviour

As agonistic interactions, we scored any type of displacement, charge, chase or physical assault (Bygott 1979; Muller & Wrangham 2004), agonistic calls, such as screams and ‘waa’ barks (Fedurek et al. 2015). We considered agonistic interactions as two distinct events if they were separated by non-aggression by at least one minute.

2.4 Statistical analysis

2.4.1 Is food calling associated with agonistic events?

We used a generalized linear model with a binomial error structure using R, version 3.1.2 (R Core Team 2014). To investigate whether the number of aggressive events was related to the occurrence of food calling, we created a model with the occurrence of the food calling (0/1) as the dependent variable, and the number of agonistic events during a feeding event as the independent variable. Food type (1: fruits [N=106]; 0: non-fruit foods [N=125]), the number of adult and late adolescent males and females, and feeding event duration (in seconds), were included in the model as additional (control) independent variables as these variables are known to correlate with chimpanzee food calling (Slocombe et al. 2010; Fedurek & Slocombe 2013). Since the number of males may be correlated with the number of aggression events on a feeding patch, we also included an interaction between the number of males and the number of agonistic events. In addition, since this might be relevant to food calling (i.e. chimpanzees are more likely to food call in the presence of others (Slocombe et al. 2010)), we included the variable (0/1) whether (N=71) or not (N=160) the feeding patch was occupied by other individuals prior to the subject animal entering it.

We then ran a linear model with a Gaussian error structure, where we included only the feeding events in which food calling occurred (N=131). In this model we used the same independent variables, and as the dependent variable we put the duration of food calling during a feeding event (s). To test the significance of both models, we used the 'anova' function in R comparing the full model against a null model comprising the same independent variables as the full model apart from 'the number of agonistic events during a feeding event' (using the 'Chisq' test and the 'F' test for the generalised linear model and the linear model respectively).

There was no collinearity between the examined independent variables (variance inflation factors of the independent variables were below 1.4). Before running the analyses, the values of all quantitative variables were z transformed into a mean of 0 and standard deviation of 1.

2.4.2 Does food calling precede or follow agonistic events?

To investigate the sequential association between food calling and agonistic events, we examined whether the production of food-associated calls preceded agonistic events or vice versa. To this end, we used a two proportions z-test and compared the proportions of food calling (0/1) that preceded and followed agonistic events within one minute. To deal with the problem of pseudo-replication, we included in this analysis only one (the last) agonistic event of each feeding event (68 of 115 agonistic events). These analyses were conducted using R, version 3.3.2 (R Core Team 2014).

Since we created two models based on the same independent variables, the α-level for significance was corrected (from 0.05 to 0.025) using Sidak's adjustment equation to control for family-wise error (Sidak 1967).

3. Results

Overall, food-associated calls were produced in 56.71% (N=131 of 231) of feeding events.

The production of food-associated calls

The full model was significantly different from the null model (Deviance=18.41, $P<0.001$). There was a positive relationship between food call production and the number of agonistic events on a feeding patch (Table 1). Agonistic events occurred more commonly during feeding events in which food-associated calls were produced (N = 109 agonistic events, Mean = 0.83, SD = 1.52) than during feeding events with no food calling (N = 6, Mean = 0.06, SD = 0.31). There was no relationship between food call production and the number males and females on the food patch, or food type (Table 1). Whether or not the subject animal entered an already occupied by others food patch did not significantly relate to food call production

(Table 1). There was no interaction between the number of males and the number of agonistic events (*P*=0.922), suggesting that these two variables predict food call production independently.

Table 1 The relationship between food call production and the investigated (independent) variables using a generalized linear model

Independent variable	**Estimate ± SE**	***z* value**	***P* value**	**95% confidence interval**
Food type	-0.081 ± 0.305	-0.265	0.791	-0.684 to 0.515
Number of agonistic events	1.493 ± 0.477	3.132	0.002	0.688 to 2.578
Number of males	0.177 ± 0.100	1.766	0.077	-0.014 to 0.383
Number of females	-0.188 ± 0.222	-0.845	0.398	-0.636 to 0.246
Feeding event duration	0.382± 0.191	2.001	0.045	0.023 to 0.780
Food patch occupancy status	0.692 ± 0.394	1.758	0.079	-0.072 to 1.480

Food calling duration

The full model was significantly different from the null model (F=47.50, *P*<0.001). There was a positive relationship between food calling duration and both the number of agonistic events and the number of males on a feeding patch (Table 2; Fig 1). There was no relationship between food calling duration and the number females or food type (Table 2). Whether or not the subject animal entered an already occupied by others food patch did not predict food calling duration (Table 2). There was no interaction between the number of males and the number of agonistic events (*P*=0.245), suggesting that these two variables predict independently food calling duration.

Table 2 The relationship between food calling duration and the investigated (independent) variables using a linear model

Independent variable	**Estimate ± SE**	***t* value**	***P* value**	**95% confidence interval**
Food type	0.096 ± 0.133	0.719	0.474	-0.168 to 0.361
Number of agonistic events	0.396 ± 0.057	6.892	<0.001	0.282 to 0.510
Number of males	0.070 ± 0.028	2.464	0.015	0.014 to 0.127
Number of females	-0.033 ± 0.069	-0.473	0.637	-0.169 to 0.104
Feeding event duration	0.270 ± 0.071	3.790	<0.001	0.129 to 0.411
Food patch occupancy status	0.052 ± 0.157	0.336	0.737	-0.257 to 0.362

Temporal relationship between food calling and agonistic events

40 of 68 agonistic events (58.8 %) were followed, while 17 (25.0 %) were preceded, by food-associated calls within one minute (two pro- portions z-test: $\chi^2 = 15.98$, df = 1, $P < 0.001$; Fig. 2).

4. Discussion

The fact that animal signals can refer to external objects or events is of considerable importance for theories of a number of disciplines, including philosophy or evolutionary approaches to anthropology and linguistics (Fedurek & Slocombe 2011; Townsend & Manser 2013; Schlenker et al. 2016). While previous studies have shown that chimpanzee food-associated calls attract others and coordinate feeding decisions (Slocombe & Zuberbühler 2005; Fedurek & Slocombe 2013; Kalan & Boesch 2015), the results of our study suggest that food calling in this species is also related to agonistic behaviour: individuals were more likely to food-call, and called for longer, during feeding events associated with aggressive interactions independent of the number of individuals on the feeding patch. Importantly, food calling followed rather than preceded agonistic events, suggesting that aggression triggers food calling rather than vice versa.

Food-associated calls have been also linked to aggression in rhesus macaques (*Macaca mulatta*) and white-faced capuchin monkey (*Cebus capucinus*). In both species the likelihood of receiving aggression was negatively related to food call production and it has been suggested that this is because individuals who refrain from announcing food discovery are subjected to aggression from group members (Hauser & Marler 1993; Gros-Louis 2004). In chimpanzees, however, food-associated calls are usually produced when the receivers of the call, and therefore potential aggressors, are already on the food patch (Fedurek & Slocombe 2013), making the food announcement hypothesis unlikely to be the dominant explanation for this behaviour. Another study on capuchins suggested that food calling promotes inter-individual spacing by signalling aggressive attitude towards co-feeders (Boinski & Campbell 1996). This spacing hypothesis, however, also appears unsuitable for chimpanzees since in this species food calling follows rather than precedes agonistic events, possibly to restore peaceful co-feeding after disruption caused by aggression.

As opposed to the number of males on a feeding patch, the number of females did not predict food calling, which seems to be consistent with previous studies on chimpanzee food calling (Slocombe et al. 2010; Fedurek & Slocombe 2013). This could be because in Eastern chimpanzees males are the more gregarious sex (Mitani 2009) and therefore males call more often either to attract other males (Slocombe et al. 2010) or oestrous females (Kalan & Boesch 2015) to food, or to coordinate feeding decisions amongst themselves (Fedurek & Slocombe 2013). However, another interpretation of this relationship is that individuals are more likely to call in the presence of males than females since males pose a higher aggression threat than females. Our results showing a positive relationship between calling and aggression are consistent with the second hypothesis. Nevertheless, there was no interaction between the number of agonistic interactions and the number of males on a feeding patch in terms of the influence of these two variables on food calling, suggesting that the effect of the former was not confounded by the effect of the latter. Furthermore, our result showing that food calling was more likely to erupt after rather than prior to agonistic events also supports the hypothesis that this behaviour is related to agonistic events. However, we encourage for more detailed studies investigating the relative importance of feeding party composition and agonistic events in food call production.

Contrary to previous studies showing that chimpanzee food calls are more likely produced when feeding on fruits compared to other types of food (Fedurek & Slocombe 2013; Kalan & Boesch 2015), we did not find this pattern in our study. However, this discrepancy between our and previous studies might be due to the different ways the data were collected for these studies. For example, we collected data on food calling occurring during the entire feeding event rather than during its initial stages (e.g. Fedurek & Slocombe 2013). Furthermore, in this study we employed a method of data collection allowing us to record data from all individuals on a feeding patch (e.g. Vogel & Janson 2007). Although this method does not focus on the behaviour of particular individuals, it is effective in establishing relationships between particular behaviours or interactions exhibited by all individuals on a feeding patch, and how they relate to the composition of the feeding group (Vogel & Janson 2007). Again, however, more detailed studies focusing on individual chimpanzees (as opposed to entire feeding groups) are required to directly explore the relationship between calling and aggression and therefore the function of these calls in relation to aggression. From a more general functional perspective, food-associated calls may allow the receiver to predict the subsequent behaviour of the caller (e.g. Smith 1977) by, for example, signalling a non-aggressive attitude (in a similar way to how these calls predict feeding duration of the caller, allowing to coordinate feeding decisions between co-feeders (Fedurek & Slocombe 2013)). However, to test the aggression-mitigation hypothesis it would be important to show that individuals that food call are indeed more likely to tolerate co-feeders in close proximity, or less likely to be involved in aggression. Furthermore, more detailed studies are needed to establish who (i.e. the victim, aggressor, or bystander) is most likely to call after an agonistic event. We consider our study as a promising starting point in this research avenue.

It would be also interesting to relate the acoustic structure of food-associated calls to different contexts associated with aggression. For example, when a dominant individual displays on a feeding tree, food calling of party members becomes noisier and higher-pitched (G. Ischer and P. Fedurek, personal observation). It is thus possible that the function of food calling in agonistic contexts is modulated by its acoustic structure – an aspect that should be investigated in the future. Since food calling often follows aggressive interactions, it is also possible that this behaviour facilitates reconciliation in a similar way as low-cost affiliative behaviours such as grooming or touching do (Fraser & Aureli 2008). In this respect, food-associated calls might function as grooming-at-a-distance vocal signals facilitating reconciliation between former opponents, or consolation by nearby individuals towards victims of aggression (De Waal & van Roosmalen 1979; Fedurek et al. 2013; Arlet et al. 2015). Again, more research is needed to investigate the mechanism behind chimpanzee food calling and its potential function in mitigating aggressive interactions.

It is also important to note that the results of our study are not incompatible with that of previous studies showing that these calls play several different roles, such as attracting others to food, facilitating feeding coordination or social bonding, and other functions (Slocombe &

Zuberbühler 2006; Slocombe et al. 2010; Fedurek & Slocombe 2013). Furthermore, other hypotheses linking food calling to aggressive interactions are feasible. For example, by calling low-ranking individuals may recruit allies that in turn may reduce the probability of receiving aggression from others. This hypothesis is not mutually exclusive with the hypotheses discussed above. Again, more research is needed to investigate the relationship between food calling and aggression.

To conclude, food calling in chimpanzees was positively associated with agonistic contexts, suggesting that the function of these calls is related to aggression. Food-associated calls, for example, might mitigate agonistic interactions or restore tolerance between co-feeders after aggression – hypotheses that should be tested in more detail by future studies. Our study adds to the growing body of literature exposing the complexity of this apparently multifunctional call.

Declaration of Competing Interests

None.

Acknowledgements

We are grateful to the management and staff of the Budongo Conservation Field Station for their support and assistance. We thank the Uganda Wildlife Authority and the Uganda National Council for Science and Technology for permission to conduct the study. We are grateful to the Royal Zoological Society of Scotland for providing core funding to the Budongo Conservation Field Station. Fieldwork was supported by the University of Neuchatel (GI) and the Swiss National Science Foundation (KZ). We thank Ammie Kalan and two anonymous reviewers for helpful suggestions and comments that greatly improved the manuscript.

References

Arlet, M., Jubin, R., Masataka, N. & Lemasson, A. 2015. Grooming-at-a-distance by exchanging calls in non-human primates. Biology Letters, **11**, 20150711.

Boinski, S. & Campbell, A. F. 1996. The huh vocalization of white-faced capuchins: a spacing call disguised as a food call? Ethology, **102**, 826-840.

Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of animal communication*. Sunderland: Sinauer Associates, Inc.

Bygott, J. D. 1979. Agonistic behaviour, dominance, and social structure in wild chimpanzees of the gombe national park. In: (Ed. by D. A. Hamburg & McCown. E R), pp. 405-428. Menlo Park:Benjamin/Cummings.

Clay, Z., Smith, C. L. & Blumstein, D. T. 2012. Food-associated vocalizations in mammals and birds: what do these calls really mean? Animal Behaviour, **83**, 323-330.

De Waal, F. B. & van Roosmalen, A. 1979. Reconciliation and consolation among chimpanzees. Behavioral Ecology and Sociobiology, **5**, 55-66.

Fedurek, P. & Slocombe, K. E. 2013. The social function of food-associated calls in male chimpanzees. American Journal of Primatology, **75**, 726-739.

Fedurek, P. & Slocombe, K. E. 2011. Primate vocal communication: a useful tool for understanding human speech and language evolution? Human Biology, **83**, 153-174.

Fedurek, P., Slocombe, K. E. & Zuberbühler, K. 2015. Chimpanzees communicate to two different audiences during aggressive interactions. Animal Behaviour, **110**, 21-28.

Fedurek, P., Machanda, Z. P., Schel, A. M. & Slocombe, K. E. 2013. Pant hoot chorusing and social bonds in male chimpanzees. Animal Behaviour, **86**, 189-196.

Fraser, O. N. & Aureli, F. 2008. Reconciliation, consolation and postconflict behavioral specificity in chimpanzees. American Journal of Primatology: Official Journal of the American Society of Primatologists, **70**, 1114-1123.

Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge: Harvard University Press.

Gros-Louis, J. 2004. The function of food-associated calls in white-faced capuchin monkeys, Cebus capucinus, from the perspective of the signaller. Animal Behaviour, **67**, 431-440.

Hauser, M. D. & Marler, P. 1993. Food-associated calls in rhesus macaques (Macaca mulatta): II. Costs and benefits of call production and suppression. Behavioral Ecology, **4**, 206-212.

Kalan, A. K. & Boesch, C. 2015. Audience effects in chimpanzee food calls and their potential for recruiting others. Behavioral Ecology and Sociobiology, **69**, 1701-1712.

Kalan, A. K., Mundry, R. & Boesch, C. 2015. Wild chimpanzees modify food call structure with respect to tree size for a particular fruit species. Animal Behaviour, **101**, 1-9.

Luef, E. M., Breuer, T. & Pika, S. 2016. Food-associated calling in gorillas (Gorilla g. gorilla) in the wild. PloS one, **11**, e0144197.

Macedonia, J. M. & Evans, C. S. 1993. Essay on contemporary issues in ethology: variation among mammalian alarm call systems and the problem of meaning in animal signals. Ethology, **93**, 177-197.

Marler, P., Evans, C. S. & Hauser, M. D. 1992. Animal signals: motivational, referential, or both. Nonverbal vocal communication: Comparative and developmental approaches, , 66-86.

Mitani, J. C. 2009. Male chimpanzees form enduring and equitable social bonds. Animal Behaviour, **77**, 633-640.

Muller, M. N. & Mitani, J. C. 2005. Conflict and cooperation in wild chimpanzees. Advances in the Study of Behavior, **35**, 275-331.

Muller, M. N. & Wrangham, R. W. 2004. Dominance, aggression and testosterone in wild chimpanzees: a test of the 'challenge hypothesis'. Animal Behaviour, **67**, 113-123.

R Core Team. 2014. R: A language and environment for statistical computing.R Foundation for Statistical Computing, Vienna, Austria.2013, .

Reynolds, V. 2005. *The Chimpanzees of the Budongo Forest: Ecology, Behaviour and Conservation*. Oxford: Oxford University Press.

Schel, A. M., Machanda, Z., Townsend, S. W., Zuberbühler, K. & Slocombe, K. E. 2013. Chimpanzee food calls are directed at specific individuals. Animal Behaviour, **86**, 955-965.

Schlenker, P., Chemla, E. & Zuberbühler, K. 2016. What do monkey calls mean? Trends in cognitive sciences, **20**, 894-904.

Sidak, Z. 1967. Rectangular confidence regions for the means of multivariate normal distributions. Journal of the American Statistical Association, **62**, 626-633.

Slocombe, K. E. & Zuberbühler, K. 2006. Food-associated calls in chimpanzees: responses to food types or food preferences? Animal Behaviour, **72**, 989-999.

Slocombe, K. E. & Zuberbühler, K. 2005. Functionally referential communication in a chimpanzee. Current Biology, **15**, 1779-1784.

Slocombe, K. E., Kaller, T., Turman, L., Townsend, S. W., Papworth, S., Squibbs, P. & Zuberbühler, K. 2010. Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. Behavioral Ecology and Sociobiology, **64**, 1959-1966.

Smith, W. J. 1977. *The Behavior of Communicating: An Ethological Approach*. Harvard University Press.

Stegmann, U. 2013. *Animal Communication Theory: Information and Influence*. Cambridge University Press.

Townsend, S. W. & Manser, M. B. 2013. Functionally referential communication in mammals: the past, present and the future. Ethology, **119**, 1-11.

Vogel, E. & Janson, C. 2007. Predicting the frequency of food-related agonism in white-faced capuchin monkeys (Cebus capucinus), using a novel focal-tree method. American Journal of Primatology, **69**, 533-550.

Figure Legends

Fig. 1. The relationship between food calling duration and the number of agonistic events. Line represents regression line and circles represent data points

Fig. 2. Proportion of food calling that preceded and followed agonistic events (*** $P<0.001$)