Regulation of vocal output by chimpanzees finding food in the presence or absence of an audience*

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Chimpanzees (*Pan troglodytes*) give both food barks and pant hoots upon encountering food and regulate their calls based upon such factors as food quantity, quality, and possibly divisibility. Although it has been determined that several species, both primate and non-primate, regulate their food calls based upon the presence or absence of an audience, this has not been systematically explored with chimpanzees. Group-housed chimpanzees were given access to either large or small quantities of food when they had either visual access to companions (Audience condition) or were visually isolated (No Audience condition). We predicted that chimpanzees would call more for larger quantities of food and more in the presence of an audience. As expected, food calling was greater for large quantities of food than small quantities. The effect of an audience was more complex. A visible audience increased the rate of food calling for a large, sharable quantity of food, yet decreased the rate for a small, non-sharable quantity. These results are consistent with the hypothesis that chimpanzee vocal expression is sensitive to social context, and that they are able to regulate the information made available to others in accordance with predicted future interaction.

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Introduction

Recent work on food-associated vocalizations (also: food calls) in primates and birds indicates that aspects of these calls are under the voluntary control of the caller (Gyger et al., 1986; Marler et al., 1986a; Hauser & Wrangham, 1987; Evans & Marler, 1991; Hauser & Marler, 1993a, 1993b; Caine et al., 1995; van Krunkelsven et al., 1996; see Cheney & Seyfarth, 1990 for a review of the voluntary nature of calling). In these cases, although the call may reflect the emotional state of the caller, some of its elements, or even the entire call, can be modified or suppressed. This information withholding in food calls may be a new avenue for the controlled exploration of capacities for the manipulation of information, including deception.

Many of the studies to date have focused on how individuals modify their food calls as food quantity or quality varies. Since individuals generally call more for larger quantities of food (Hauser & Wrangham, 1987; Clark & Wrangham, 1993; Hauser et al., 1993; Caine et al., 1995) or better quality of food (Marler et al., 1986a; Elowson et al., 1991; Caine et al., 1995, but see Roush & Snowdon, 2000), it is assumed that this increase reflects the emotional state of the caller and reflects excitement at the presence of a food bonanza. However, some of these calls may be manipulated by the caller, as evident from possible examples of punishment for food discoverers who fail to advertise their find.

Hauser and Marler (1993b) examined food calling and aggression in rhesus monkeys (*Macaca mulatta*) on Cayo Santiago and concluded that failure to call was linked with greater aggression and food loss than was calling upon food discovery. However, the link between dominance rank and/or previous history of aggression and food calling is unknown. While monkeys who failed to call did subsequently receive more aggression, it is also possible that those monkeys who tended to receive aggression had learned to suppress calls.

Furthermore, although most species' food calling rates vary, not all studies have found variation in food calling with respect to food quantity and quality, indicating that food calling may be modifiable by the caller. For instance, whether or not bonobos (*Pan paniscus*) give food calls does not vary with food quantity or quality (van Krunkelsven et al., 1993), indicating that although food may elicit calls, neither quantity nor quality are an issue. Among cotton top tamarins (*Saguinus oedipus*), calling rate does not vary with food quantity, but is affected by whether or not the adults have offspring (Roush & Snowdon, 2000).

Further studies have found that food divisibility, rather than quantity or quality, may elicit variation in food calls. Both house sparrows (*Passer*

domesticus; Elgar, 1986) and chimpanzees (*Pan troglodytes*; Hauser et al., 1993) call more for a divisible resource than an indivisible one when food quantity is held constant. This would indicate that animals call especially when the food source cannot easily be monopolized or stolen by another, allowing the caller to maximize access to the food. However, it is also possible that the caller has the "illusion" of having more food in the divisible than in the indivisible case (Hauser et al., 1993).

Some call variation reflects physical characteristics other than those of the discovered food, such as social factors. Modification of food calling rate based on social factors has been well documented in chickens (*Gallus gallus)* and several primate species. Roosters have a distinct food-associated call (Evans & Marler, 1994) which they use more in the presence of hens than in the presence of other roosters or in the absence of an audience (Evans & Marler, 1994). Furthermore, near unfamiliar hens, roosters will food call to non-food items, something they do not do in the presence of familiar hens or other roosters, or when no audience is present (Marler et al., 1986b). Since food calling will attract a female (95% of the time females attracted to food by a rooster's food calls consume the food item), this behavior shows discrimination and potentially deception by the rooster.

Red-bellied tamarins (*Saguinus labiatus*) call more frequently when group mates are out of view, indicating that more than food competition is initiating these calls (Caine et al., 1995). Caine et al. (1995) hypothesize that for this small-bodied species, attracting group members to aid in predator protection outweighs increased food competition. Cotton-top tamarins called more when in proximity to other group members, but did not vary their calling rates dependent on whether their mates were present (Roush & Snowdon, 2000). Here, food calling may function as a spacing mechanism, similarly to that proposed in field studies (*Ateles geoffroyi*: Chapman & Lefebvre, 1990; *Cebus capucinus*: Boinski & Campbell, 1996). Captive bonobos appear to suppress their food calls when an audience is present, perhaps to avoid competition (van Krunkelsven et al, 1996). In the field, there are anecdotes of chimpanzees suppressing their food calls until an audience, who may steal the food, has left (Goodall, 1986).

Somewhat surprisingly, no previous studies have rigorously examined how chimpanzees alter food calling based on social context. Since there exists anecdotal evidence that chimpanzees deceive others (*e.g.* by not giving away the presence of food to ignorant group mates; Menzel 1971; de Waal, 1982, 1992), and modify their response to calls (*e.g.* the likelihood of response to the call of

an unfamiliar male depends upon group composition; Wilson et al., 2001), it is likely that chimpanzees do alter food calls contingent upon an audience. We altered the presence of a conspecific, familiar audience in conjunction with food quantity in chimpanzees in order to determine how social factors interact with physical ones to modify the chimpanzee's food calling behavior. As the audience consisted of the subject's own community, reactions were likely to be made with respect to future social consequences.

We predicted that individuals would call more in situations with larger quantities of food, as found previously (see above). In chimpanzees, this may serve to advertise opportunities for food sharing. We also predicted that calling would increase in situations in which an audience was present, for one of two reasons. First, chimpanzees are intensely social, and the presence of an audience may arouse them and cause them to vocalize more frequently regardless of food quantity. We will call this the Social Facilitation Hypothesis. Second, chimpanzees may vocalize to announce quantities of food large enough to be shared with others, yet fail to call for smaller quantities so as to keep this food for themselves. In this case, audience would affect calling only if food is abundant, and calling would be absent or suppressed for smaller quantities. This we will call the Information Manipulation Hypothesis. One way to distinguish between these two hypotheses is to investigate the interaction between vocal responses to different food quantities and the presence of an audience. The Social Facilitation Hypothesis predicts a similar stimulating effect of audience on calling for large and small food quantities, whereas the Information Manipulation Hypothesis predicts that audience differentially affects calling for large and small quantities.

Methods

Subjects

Chimpanzees used for the experiment were housed in a single social group at the Yerkes Primate Center Field Station in Lawrenceville, Georgia, USA. Thirteen chimpanzees were involved in the study, out of 23 housed in the colony (we only utilized those individuals willing to enter the testing facility). They included 1 adult male (age 30), 5 adult females (ages 14 to 29), 2 juvenile males (ages 6 and 7), 3 juvenile females (ages 5 to 7), 1 infant male (age 5) and 1 infant female (age 4). All juveniles and infants lived with their mothers.

Among the adults, there was one close, non-kin, relationship; the youngest adult female was the adoptive daughter of one of the oldest adult females. This relationship is classified as a kin relationship. Juveniles and infants are classified as immatures for all analyses.

Rank was divided into 3 categories, high, which included the alpha male and alpha female, medium, which 6 mid-ranking adult and juvenile females, and low which included 2 juvenile females and 3 juvenile males. Rank was independently determined from observation sessions run twice weekly on the group. These 90 minute sessions included scan samples every 10 minutes for affiliative and contact behaviors, and ad libitum collection of aggressive or other dominance behaviors. Rank within the group was very stable during the period of testing.

Housing

Subject's daily housing consisted of a 24 by 30 m outdoor corral and an indoor quarters which was divided into 4 rooms. Tests were conducted in the largest room of the indoor quarters. A 30 × 40 cm window was installed in the larger guillotine door connecting this room with the outdoor enclosure. The window (which was too small for all but the smallest infant to climb through) could be either left open or covered with a panel made either of transparent Plexiglas or of opaque latex. When a subject was being tested, the rest of the colony remained outdoors.

Every day subjects received Purina Monkey Chow twice, once in the early morning (which remained available throughout the day), and again in the early evening. Fruits were provided daily at about 11:30 hours. Running water was available *ad libitum*. This feeding schedule was maintained regardless of the day's testing.

Experimental Procedures

Tests were run approximately twice a week from February 1993 to January 1994. The majority of subjects tested were adult females and their dependent offspring, who always accompanied them (as would be true in any situation, including in the field). One juvenile female accompanied the adult male on approximately half of his low-food tests, and this male was not prevented from accompanying estrous females, although this occurred only occasionally. Food was presented in an opaque box which the chimpanzee accessed by reaching through the bars of the cage to remove the lid. Food was always carried into the building in an opaque bag of the same size and weight to prevent the chimpanzees

from guessing what type of test would ensue. Every chimpanzee willing to enter the testing area was tested in every daily testing round.

Rounds were of two types, low-food rounds and high-food rounds. Only one type of round was done per testing day. Low-food rounds consisted of a small but desirable amount of food (*e.g.* a couple of peanuts) in every test on separate individuals, whereas high-food rounds consisted of a large amount of food (*e.g.* a full box with at least 15 apples or oranges) for a single, randomly selected, test, while all remaining tests in the same round consisted of the same small amount of food as in low-food tests. For the chimpanzees, it was unpredictable who would be the recipient of the food bonanza in a high-food round of testing. During low-food tests, including those inserted in the high-food rounds, subjects were allowed to stay in the room for 5 minutes, whereas for high-food tests, subjects could stay for up to 15 minutes. This was necessary as the chimpanzees required longer to consume the larger quantity of food. In all tests, chimpanzees were free to leave at any time by pressing a button which would alert the experimenter to open the door. Early exits, combined with different frequencies of testing for every individual, led to the chimpanzees differing in the amount of time they spent in each type of test.

Testing rounds were run under three different conditions. In the No Audience condition an opaque window was in place between the testing area and the outdoor enclosure, which prevented visual and tactile contact between the test subject(s) and the remainder of the colony. Second was the Clear Condition, in which a transparent window was in place and the subject was tactilely but not visually separated from the remainder of the colony. Third was the Open Window condition, in which there was no panel in the window between the subject and the rest of the colony, providing full visual and limited tactile contact. This was also the condition under which even the softest calls inside the building could be heard outside. The window was small enough that the audience members could not come through the window, but they could insert arms or throw objects inside. Under all conditions, the subjects and the group were in auditory contact. Given the strength of the chimpanzee's voice, auditory isolation at close range is virtually impossible to achieve. In addition, our chimpanzees would never have experienced this condition before.

Data were collected using a Super-VHS video camera placed inside the building, aimed at the food box and the indoor cage. The time display on the video camera was run continuously, allowing all times to be recorded accurately to the nearest tenth of a second. After each test, any commentary about the trial was dictated into the microphone of the camera by the experimenter.

In transcribing the video tapes, an observer familiar with chimpanzee behavior collected data on the number of individual pieces of food consumed by each subject during a trial. Data were also collected on the rate of food calling from the video tapes (by ear), which was calculated as the number of food calls an individual gave per hour they participated in each test type. Although chimpanzees have two distinct food calls, grunts and hoots (Goodall, 1986), no hoots were recorded. Accordingly, only food grunts were counted. Finally, each test was categorized by whether or not the discovery was accompanied by vocalization, which we considered to be vocalization given immediately upon opening the food box for the first time.

Finally, data were collected on the degree to which the subject, while uttering food calls, oriented their body towards the window behind which lay the remainder of the colony. Due to the layout of the room, the chimpanzees collected food from the box with their back facing the window. Thus subjects' orientation towards the window required them to actively orient away from the food box. We categorized orientation as oriented towards the window: (1) not at all, (2) somewhat, (3) mostly, or (4) completely.

Statistics done included repeated-measures analysis of variance and t-tests. All p-values are two-tailed.

Results

In the following analyses, the Clear and Open Window conditions were combined into the Audience condition, based upon the presence of visual contact between the subject and the audience. Moreover, these two conditions were not found to differ significantly.

A categorization made by ear indicates that food related vocalizations roughly divided between soft food grunts (58.5% of food calls; Goodall, 1986), food barks (29.0% of food calls; Goodall, 1986), soft, "emmm" grunts (10.6% of food calls), which may be similar to the "double-grunt" in Goodall, 1986, which indicated contentment and were not necessarily linked to food, and calls that appeared to be a mixture of the above (1.9% of food calls). Other food related vocalizations, including "aaa" calls, pant-hoots, and screams have been documented in wild chimpanzees (Goodall, 1986; Clark, 1993), but were not heard in this study. Analysis was done based upon the aggregate of vocalizations, without distinction as to different call types.

Discoveries with Food Calling

Food calling was analyzed to see if calling upon food discovery varied across the audience conditions and food quantities. As explained above, the Clear and Open Window conditions were combined into an Audience condition and compared with the No Audience condition, in which an opaque panel covered the window. The measure used here is the percentage of food discoveries accompanied by food calls regardless of the amount or duration of calling. Analysis was done using a repeated measures analysis of variance (ANOVA) with audience condition (audience visible versus absent) and test type (high versus low food quantity) as the within-subjects factors, and age class (adult versus immature) and rank (high, medium, and low) as a between-subjects factor. For the percentage of discoveries with food calls, see Table 1.

There was no effect of audience condition on whether or not chimpanzees called upon discovery of food ($F_{1,9} = 0.42$, NS). There was a significant effect of the amount of food such that subjects called more when discovering larger than smaller quantities ($F_{1,9} = 29.87$, $p < 0.001$). There was no interaction between food quantity and audience condition ($F_{1,9} = 0.008$, NS). There was also no interaction between the subject's age category with either audience condition ($F_{1,9} = 0.20$, NS) or food quantity ($F_{1,9} = 0.78$, NS). Finally, there was no interaction between the subject's rank category and either audience condition ($F_{2,8} = 0.658$, NS) or food quantity ($F_{2,8} = 0.488$, NS)

Rate of Food Calling

The rate of food calls was calculated as the number of individual calls (counted by ear from the video recording) that an individual produced under a given

Table 1. The number of food discoveries in each category accompanied by vocalization (mean ± standard deviation).

	Low Food/ Audience	Low Food/ No Audience	High Food/ Audience	High Food/ No Audience
Adults	1.08 ± 1.81 %	7.22 ± 8.77 %	61.17 ± 25.22 %	58.33 ± 37.64 %
Immatures	0.78 ± 1.10 %	3.98 ± 5.56 %	35.00 ± 37.91 %	50.00 ± 50.00 %
All	0.95 ± 1.46 %	5.75 ± 7.33 %	49.27 ± 37.18 %	54.55 ± 41.56 %

A food discovery was the moment a chimpanzee opened the food bin and saw what quantity of food was hidden within the bin. The category Low Food is a few peanuts while High Food is 15 whole fruits. The Audience consisted of visible member(s) of the subject's home group, while in the No Audience condition the subject was visually (although not vocally) isolated from the group.

condition divided by the number of hours the individual spent under that condition. In contrast to the previous measure, which concerns merely the presence or absence of calling, this measure reflects overall vocal output. Food calling rate was analyzed across four conditions: low food with audience, low food without audience, high food with audience, and high food without audience. Similar to the above analysis, calling rate was subjected to a repeated measures ANOVA with test type (high versus low food quantity) and condition (audience versus no audience) as within-subjects factors measured across each individual subject and age class (adult versus immature) and rank (high, medium, and low) as between-subjects factors. For the actual rate of food calling, see Table 2, and for a visualization, see Figure 1.

There existed a strong, overall effect of the amount of food on the frequency of food calling, with subjects calling more frequently in high-food than low-food tests ($F_{1,10} = 53.70$, $p < 0.0001$). Whereas we found no overall effect of the presence of an audience on the frequency of food calling ($F_{1,10} = 0.003$, NS), there existed a significant interaction effect such that in high-food tests, chimpanzees vocalized more frequently with an audience present, but in low-food tests, they vocalized less frequently with an audience present (Figure 1; $F_{1,10} = 11.15$, $p = 0.007$). There was no significant effect of the subject's age with either audience condition ($F_{1,10} = 2.88$, NS) or food quantity ($F_{1,10} = 0.004$, NS). There was also no significant effect of the subject's rank with either audience condition ($F_{2,9} = 0.818$, NS) or food quantity ($F_{2,9} = 1.075$, NS).

Orientation of the Caller

Based upon the orientation categories discussed previously (orientation towards the window: not at all; somewhat; mostly, or completely), an individual index was created to classify the mean orientation of the subject during food calling. The number of vocalizations by an individual oriented 'not at all' towards the

Table 2. The number of food-related vocalizations per hour (mean ± standard deviation) within each category. Categories are the same as those described in Table 1.

	Low Food/ Audience	Low Food/ No Audience	High Food/ Audience	High Food/ No Audience
Adults	1.29 ± 1.02	14.66 ± 19.83	42.37 ± 12.57	37.03 ± 19.90
Immatures	0.88 ± 1.34	5.83 ± 9.18	41.29 ± 21.15	27.74 ± 20.23
Total	1.08 ± 1.16	10.24 ± 15.07	41.83 ± 16.60	32.38 ± 19.74

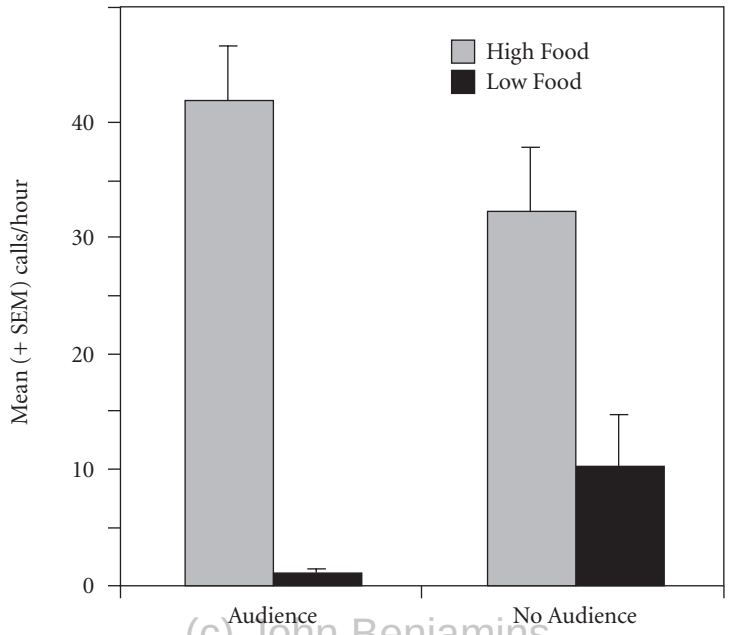

Figure 1. The effect of the interaction between audience presence or absence and food quantity on the overall number of food-related vocalizations per hour. For high-food tests, chimpanzees vocalize more frequently with an audience present while for low-food tests, chimpanzees vocalize less frequently with an audience present.

window multiplied by one, 'somewhat' multiplied by two, 'mostly' multiplied by three, and 'completely' multiplied by four. This sum was then divided by the total number of vocalizations to provide an index of how strongly food callers oriented towards the outside door behind which was the rest of the group, either visible (Audience condition) or invisible (No Audience). There were not enough calls in the low-food condition to calculate the same index. Within the high-food condition, there was no significant difference in the orientation of the caller between the Audience and No Audience conditions (Paired t-test, $t = 0.13$, $df = 12$, NS).

Discussion

A number of species modify their food-related vocalizations based on varying conditions, and chimpanzees are no exception. It has previously been found

that chimpanzees' food vocalizations vary depending on different factors relating to the food itself, such as quantity, quality, or perhaps divisibility (Hauser & Wrangham, 1987; Clark & Wrangham, 1993; Hauser et al., 1993). In our study, as in these others, chimpanzees call at considerably higher rates for large quantities of food than for small quantities.

There are two possible non-exclusive explanations why chimpanzees call at a higher rate when food is abundant. First, chimpanzees may become more excited in the presence of a large quantity of food, and hence be more likely to vocalize. This motivational explanation may account for the chimpanzees' response, but does not explain the function of calling. Second, perhaps food calling serves to alert others to the presence of enough food to share. Chimpanzees' tendency to vocalize more for divided than undivided portions of food when quantity is held constant supports this functional view (Hauser et al., 1993).

Although the effect of an audience on food vocalizations has been documented in some avian species (Marler 1986a, 1986b; Evans & Marler, 1994) and primates (Hauser and Marler, 1993a. 1993b; Caine et al., 1995; Van Krunkelsven et al., 1996; Roush & Snowdon, 2000), it has not been examined in chimpanzees. This is surprising given that chimpanzees are generally considered capable of altering their behavior in the presence of others. We looked at the effect of a familiar audience on the chimpanzee's food vocalizations to see whether or not there was evidence for regulation of food calls. As proposed in the Introduction, food calling may increase with an audience for two reasons, which we labeled the Social Facilitation Hypothesis and the Information Manipulation Hypothesis.

Our study found no effect of audience on whether or not initial food discoveries were accompanied by vocalizations. This may be due to the individuals entering such a high state of excitement upon the discovery of food, especially when presented in a large quantity, that the calling is insuppressible. Anecdotal evidence indicates that vocal suppression may be quite difficult for the chimpanzee. Goodall (1986) witnessed a male placing his hands over his mouth as if in an attempt to stifle calls he uttered upon the discovery of a large quantity of bananas. If this is the case, one would expect that control over vocalizations improves once the presence of food is not longer a surprise. Hence our additional analysis of overall calling rates.

The data indicate that if calling output is measured in greater detail, as a rate of calls per time unit, there are indeed signs of regulation, and these signs support the Information Manipulation Hypothesis. The effect of a visible

audience was to increase the calling rate for a large, sharable quantity of food, yet decrease it for a small, non-sharable amount. These opposite effects seem to reflect the interplay between cooperative (i.e. food-sharing) and competitive (i.e. food monopolization) tendencies. Food calling may serve to attract other group members when there is enough food for all. This may allow the subject to gain the goodwill of its companions and future return-benefits, both of which may be important within the chimpanzee's "service economy" (de Waal, 1982; 1997). However, when there is only enough food for the discoverer itself, call withholding may be the better strategy, allowing the individual a chance to eat the food before others come to compete for it.

The orientation of the subject during food calling did not vary between the Audience and No Audience condition when high quantities of food were available. Callers are oriented mostly away from the window, indicating that even when the audience was visible, the caller was not necessarily facing them to vocalize. Such a result, however, may be due to the fact that the food container was placed such that food acquisition required the chimpanzee's back to be towards the window. There was also no effect of either age of subject or rank in any of the conditions. This may indicate that the responses we measured are independent of age or social factors.

In sum, our data support the Information Manipulation Hypothesis over the Social Facilitation Hypothesis. Even though these hypotheses are not mutually exclusive, it appears that chimpanzees are manipulating information within the bounds of their natural food-related arousal. Food calling at a higher rate for large quantities of food when there is an audience present may invite others to join in while advertising the caller's generosity (and indeed we observed a small number of cases of voluntary food transmission between the owner and the audience through the small window). It is unlikely that food calling is solely a result of social facilitation, as calling behavior did not increase or decrease as a simple function of audience presence or absence. These results are consistent with information withholding since subjects appeared to restrict their calling when they stood the greatest chance of losing the food.

References

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

Caine, N. G., Addington, R. L., and Windfelder, T. L. (1995). Factors affecting the rates of food calls given by red-bellied tamarins. *Animal Behaviour, 50*, 53–60.

Chapman, C. A., and Lefebvre, L. (1990). Manipulating foraging group size: spider monkey food calls at fruiting trees. *Animal Behaviour, 39*, 891–896.

Cheney, D. L., and Seyfarth, R. M. (1990). *How monkeys see the world: Inside the mind of another species*. Chicago: University of Chicago Press.

Clark, A. P., and Wrangham, R. W. (1993). Acoustic analysis of wild chimpanzee pant hoots: do Kibale Forest chimpanzees have an acoustically distinct food arrival pant hoot? *American Journal of Primatology, 31*, 99–109.

de Waal, F. B. M. (1982). *Chimpanzee Politics: Power and sex among apes*. Baltimore: The Johns Hopkins University Press.

de Waal, F. B. M. (1992). Intentional deception in primates. *Evolutionary Anthropology, 1*(3), 86–92.

de Waal, F. B. M. (1997). The chimpanzee's service economy: Food for grooming. *Evolution and Human Behavior, 18*, 375–386.

Elgar, M. A. (1986). House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. *Animal Behaviour, 34*, 169–174.

Elowson, A. M., Tannenbaum, P. L., and Snowdon, C. T. (1991). Food-associated calls correlate with food preferences in cotton-top tamarins. *Animal Behaviour, 42*, 931–937.

Evans, C. S., and Marler, P. (1991). On the use of video images as social stimuli in birds: audience effects on alarm calling. *Animal Behaviour, 41*, 17–26.

Evans, C. S., and Marler, P. (1994). Food calling and audience effects in male chickens, *Gallus gallus*: their relationships to food availability, courtship, and social facilitation. *Animal Behaviour, 47*, 1159–1170.

Goodall, J. (1986). *The Chimpanzees of Gombe*. Cambridge, Massachusetts: The Belknap Press of Harvard University Press.

Gyger, M., Karakashian, S. J., and Marler, P. (1986). Avian alarm calling: Is there an audience effect? *Animal Behaviour, 34*, 1570–1572.

Hauser, M. D., and Marler, P. (1993a). Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors. *Behavioural Ecology, 4*(3), 194–205.

Hauser, M. D., and Marler, P. (1993b). Food-associated calls in rhesus macaques (*Macaca mulatta*): II. Costs and benefits of call production and suppression. *Behavioural Ecology, 4*(3), 206–212.

Hauser, M. D., Teixidor, P., Fields, L., and Flaherty, R. (1993c). Food-elicited calls in chimpanzees: effects of food quantity and divisibility. *Animal Behavior, 45*, 817–819.

Hauser, M. D., and Wrangham, R. W. (1987). Manipulation of food calls in captive chimpanzees. *Folia primatologica, 48*, 207–210.

Marler, P., Dufty, A., and Pickert, R. (1986a). Vocal communication in the domestic chicken: I. Does a sender communicate information about the quality of food referent to a receiver? *Animal Behaviour, 34*, 188–193.

Marler, P., Dufty, A., and Pickert, R. (1986b). Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver? *Animal Behaviour, 34*, 194–198.

Roush, R. S., and Snowdon, C. T. (1999). The effects of social status on food-associated calling behaviour in captive cotton-top tamarins. *Animal Behaviour, 58*, 1299–1205.

van Krunkelsven, E., Dupain, J., van Elsacker, L., and Verheyen, R. F. (1996). Food calling by captive bonobos (*Pan paniscus*): an experiment. *International Journal of Primatology, 17*(2), 207–217.

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