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Maternal food calling in domestic hens: influence of feeding context

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Abstract

The aim of this study was to understand the relationship between production of food calls by maternal hens and food context. In a series of experiments with broody hens, we manipulated quality of items, quantity of food, food experience and dispersion of food items. We measured the frequency of food calling during standardized tests. Our results show that all the variables tested had significant effects on food calling. These results present some similarities and some discrepancies with previous reports on food calling by cockerels. ***To cite this article: A.-M. Wauters, M.-A. Richard-Yris, C. R. Biologies 326 (2003).***

Résumé

Le cri d'offrande alimentaire chez la poule maternelle : influence du contexte alimentaire. Cette étude se propose de permettre de mieux comprendre l'influence du contexte alimentaire sur l'émission du cri d'offrande alimentaire chez la poule domestique maternelle. Des expériences ont été menées afin de tester successivement différentes propriétés inhérentes aux aliments : leur qualité, leur quantité, leur répartition, ainsi que l'expérience qu'en ont les poules. La fréquence d'émission du cri a été mesurée pour chacun des tests effectués. Nos résultats montrent que toutes les variables testées ont des effets significatifs sur l'émission de cette vocalisation. ***Pour citer cet article : A.-M. Wauters, M.-A. Richard-Yris, C. R. Biologies 326 (2003).***

Keywords: Food call; *Gallus gallus domesticus*; feeding context; maternal behaviour

Mots-clés : cri d'offrande alimentaire ; *Gallus gallus domesticus* ; contexte alimentaire ; comportement maternel

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Différentes espèces de primates non humains et d'oiseaux possèdent au sein de leur répertoire de communication des vocalisations particulières, appelées cris d'offrande alimentaire. Chez le poulet, sauvage comme domestique, le cri d'offrande consiste en une série de sons pulsés délivrés à intervalles réguliers. Ce sont principalement les coqs et les poules maternelles qui l'émettent en présence d'aliment, attirant alors vers eux des conspécifiques avec lesquels ils partagent des liens particuliers : le coq émetteur est rejoint

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par des femelles de son groupe, alors que la poule maternelle regroupe autour d'elle ses jeunes qui viennent picorer auprès d'elle.

Chez le mâle, comme chez la femelle maternelle, des liens ont pu être mis en évidence entre le contexte alimentaire et le taux d'émission du cri d'offrande. Ainsi, on sait qu'ils émettent d'autant plus de cris d'offrande qu'ils apprécient l'aliment qui leur est proposé et qu'ils ont faim (tout du moins si l'aliment présenté n'est pas hautement appétant).

Toutefois l'ensemble des paramètres liés au contexte alimentaire général de l'émission n'a jamais été analysé en détail chez cette espèce. Or, chez différentes espèces de primates et d'oiseaux, l'émission du cri d'offrande est influencée par le degré de divisibilité de l'item découvert (chimpanzé, moineau) ou par la quantité d'aliment découverte (macaque rhésus, chimpanzé, singe araignée).

Cette étude se propose donc d'évaluer, au travers de différentes expériences, l'influence de paramètres liés au contexte alimentaire sur l'émission du cri d'offrande chez la poule maternelle. Nous avons ainsi testé successivement l'influence des facteurs suivants sur l'émission du cri d'offrande : la qualité des items alimentaires (expérience 1) ; le degré d'expérience qu'a la poule de l'aliment (expérience 2) ; la quantité d'aliment (expérience 3) ; la dispersion de l'aliment (expérience 4).

Les poules ont été testées en présence de leurs poussins lorsqu'ils étaient âgés de quatre à huit jours. Selon les cas, les tests ont été menés dans une cage test similaire à la cage d'élevage (expériences 1 et 3), dans un *open field* (expériences 2 et 4). Chaque test durait 3 min et proposait un ou plusieurs items alimentaires.

Tous les tests ont été enregistrés afin de comptabiliser le nombre de cris d'offrande émis sur chaque item.

Expérience 1. Afin de tester si la qualité de l'aliment pouvait moduler l'émission du cri d'offrande, nous avons proposé successivement aux poules trois items différents : cinq vers de farine placés sur 100 g de bouillie ; leur aliment habituel (mélange de blé et de « démarrage poussin ») ; des copeaux de bois. Les poules ont émis significativement plus de cris d'offrande en présence (a) d'un item alimentaire qu'en présence d'un item non-alimentaire (les copeaux) ou (b) d'aliments très appréciés (les vers de farine et la bouillie) qu'en présence de leur aliment habituel.

Expérience 2. Jusqu'à présent, les poules ont été testées en présence d'items consommables et non répulsifs ; voyons comment elles réagissent face à un aliment connu comme mauvais. En l'absence de leurs poussins, on habitue deux lots de poules à reconnaître un même aliment comme étant bon (lot A) ou mauvais – grâce à l'adjonction de quinine – (lot B). Puis, les poules sont testées en présence de leurs jeunes et de l'aliment que ces derniers ne connaissent pas. Lors de ce test, les poules du lot B ont émis significativement moins de cris d'offrande que celles du lot A. Le comportement des poules des deux lots était différent : les poules du lot B picoraient moins l'aliment et exploraient davantage l'environnement ; ceci pouvant tendre à garder les poussins loin de l'aliment connu comme mauvais.

Expérience 3. Après avoir testé différents aspects qualitatifs des aliments, voyons si la poule maternelle, comme certains primates, module son émission de cris d'offrande en fonction de la quantité de nourriture découverte. Pour répondre à cette question, nous avons confronté chaque poule à un test de choix, durant lequel deux mangeoires identiques, mais comportant respectivement 30 et 120 g d'un même aliment lui étaient présentées. L'observateur a noté le nombre de cris d'offrande émis, la mangeoire vers laquelle l'émission était dirigée, quelle mangeoire induisait le premier picorage et si la poule picorait dans chaque mangeoire. Si le premier picorage n'était pas dirigé préférentiellement vers la mangeoire contenant le plus d'aliment, il s'avère que la majorité des poules a picoré dans les deux sources de nourriture et que les femelles ont émis significativement plus de cris d'offrande face à la mangeoire contenant 120 g que face à celle n'en contenant que 30 g.

Expérience 4. Nous venons de voir que les poules maternelles étaient sensibles à la quantité d'aliment découvert, mais modulent-elles également leur émission de cris d'offrande en fonction de la répartition d'une même quantité d'aliment. Pour le savoir, nous avons testé les animaux dans une enceinte circulaire dans laquelle étaient disponibles 400 g d'aliment répartis, soit dans une seule mangeoire – test A –, soit dans cinq mangeoires plus petites – test B. Le nombre de cris d'offrande émis face à chaque mangeoire a été noté. Il apparaît que les poules ont émis davantage de cris d'offrande lorsque l'aliment était proposé de

façon dispersée que lorsqu'il était concentré en une même source. Toutefois, ce résultat reste difficile à interpréter, puisqu'une corrélation positive existe entre le nombre de mangeoires visitées et le nombre de cris d'offrande émis lors du test B. Trois hypothèses pourraient expliquer ce phénomène : (1) les poules pourraient estimer que les cinq petites mangeoires comportent une quantité supérieure d'aliment qu'une seule grande mangeoire ; (2) la tendance exploratoire des poules pourrait être stimulée par la multiplicité des sources d'aliment, induisant alors un surcroît d'émission ; (3) finalement, la différence d'émission enregistrée entre ces deux situations pourrait résulter d'un facteur inhérent au comportement des poussins. En effet, lors du test B, les jeunes pouvaient, à certains moments au moins, continuer à picorer dans une mangeoire alors que leur mère s'éloignait déjà vers une autre. Or, nous avons pu démontrer par ailleurs que les poules maternelles en présence d'aliment émettaient davantage de cris d'offrande lorsque leurs petits étaient éloignés d'elles.

À la lumière de ces différentes expériences, il apparaît de prime abord que l'émission du cri d'offrande alimentaire, chez la poule maternelle, est influencée par un ensemble de facteurs directement ou indirectement liés au contexte alimentaire. De plus, cette étude nous permet de mettre en avant à la fois des similitudes et des divergences entre les facteurs impliqués dans l'émission du cri d'offrande chez la poule maternelle d'une part et chez le coq d'autre part. Ainsi, mâles comme femelles émettent davantage de cris d'offrande en présence d'aliment qu'en présence d'items non consommables. Toutefois, confrontés à cette dernière situation, il apparaît que les mâles émettent plus fréquemment le cri d'offrande que les femelles. Ce phénomène pourrait être dû à une ritualisation plus importante de l'émission chez le coq et/ou à une sensibilité accrue de la poule maternelle à répondre à la présence de nourriture par du cri d'offrande.

Par ailleurs, la qualité des items alimentaires proposés influence grandement le taux d'émission du cri. La présence de vers de farine induit notamment, tant chez le mâle que chez la femelle, une émission soutenue de la vocalisation d'offrande. Le degré d'attractivité des vers pourrait tenir de plusieurs de leurs caractéristiques propres, comme leur forme, leur mobilité, mais également leur capacité de dispersion, puisque, comme on a pu le voir, une ressource alimentaire induit une émission plus élevée lorsqu'elle est divisée que lorsqu'elle est compacte.

Dans le cas d'une source alimentaire dispersée, la modification de l'environnement pourrait induire une stimulation des tendances exploratoires des animaux, au moins chez le coq, puisque comme on l'a vu précédemment d'autres facteurs liés au comportement des poussins pourraient influencer l'émission de la poule maternelle.

Il serait également intéressant de pouvoir comparer nos données résultant de l'expérience 3 à une étude similaire menée chez le coq. Ceci permettrait de savoir si la fonction nutritionnelle du cri d'offrande du mâle est, comme l'affirment certains auteurs, largement symbolique, facilitant les interactions sexuelles ou si, selon d'autres, le cri d'offrande du coq est effectivement un cri associé à la nourriture.

Néanmoins, chez la poule maternelle, il apparaît que l'émission du cri d'offrande traduit très clairement la tendance de la mère à partager des items qu'elle perçoit, du fait de son expérience, comme consommables.

1. Introduction

Food-associated calls have been reported in many field and laboratory studies of social non-human primates (see [1] for a review) and birds including house sparrows [2], cliff swallows [3], ravens [4] and several gallinaceous birds [5–7].

Food-associated vocalizations have been of interest for research addressing proximate questions, especially efforts to understand the meaning of animal signals.

Like all gallinaceous birds, chickens have a large vocal repertoire [8], which includes a call produced by both male and female upon discovering food.

Food calls of domestic and red jungle fowl chickens consist in a series of pulse like sounds delivered at almost regular intervals [8–10]. Food calls differ clearly from other calls [11] and are easily identified by human ear [12]. These rhythmically repeated calls are generally uttered when a bird is frequently picking up and dropping either edible or inedible objects that are not usually swallowed [13].

Descriptive studies have reported that these calls are produced mainly by cockerels and broody hens

with chicks, but can sometimes be emitted by non-broody hens [14–16] and more rarely by chicks [17]. Several studies reported that this vocalization attracts other foragers to the food caller site. Thus, food-calling cockerels attract hens to their vicinity [12,15] and food-calling maternal hens attract chicks to their mother's beak [9,18]. Recently, Evans and Evans [19] showed that cockerels' food calls were functionally referential, as hens responded to playbacks of food calls with anticipatory feeding movements.

In chickens, the relationship between feeding context and utterance of food calls has been underlined in several studies. In cockerels, previous experiments have demonstrated that food calling varies with type of object available to the male. For example, Marler et al. [12] measured food calling of cockerels when presented with various food items (mealworm, pea or peanut) or non-food items (nutshell). Many food calls were given to mealworm and pea, whereas fewer calls were given to peanut and nutshell. Similarly, under semi-naturalistic conditions, Gyger and Marler [20] showed that in males animal objects elicited the most rapid calling, when vegetable objects or mash stimulated only moderate call production. However, in this study, 45% of all calling occurred when no object was present. Similarly, the amount of food calling with non-food items reached more than a third of the amount of food calling with mealworm (34% and between 38 and 68%, respectively, in the studies of Marler et al. [12] and Van Kampen and Hogan [21]). Food calling is not limited to ingestible items, but it is also associated with stimuli that have in the past reliably predicted the presence of food [11].

In maternal hens, Wauters et al. [16] showed that food calling really reflected the caller's food preferences estimated during choice tests. The more a maternal hen preferred a food type, the more it uttered. Moreover, the number of food calls uttered by maternal hens is modulated by the physical structure of the food item, as they utter significantly more food calls when a food type was pulverized or mashed than when it was presented in pellets [16]. Food quality could be learnt by birds, but at present authors never tried to modify the palatability of food items and thus the experience chickens have.

Food calling is also affected by the bird's state of hunger. The hungrier the caller, the more food calls it utters. This is true for cockerels [11,21] as well as for maternal hens [16], although, in this latter case, the influence of hunger depends on the type of food.

However, other parameters related to the general feeding context as available quantity or dispersion of food have rarely been investigated in detail in chickens. For example, van Kampen and Hogan [21] tested males in two situations: a 'rich' condition, which provided three mealworms, extra food sharing and normal food scattered around the edges of the arena, versus a 'poor' condition, with only one mealworm in addition to the normal food. They observed that males performed food calling more frequently in the rich condition than in the poor condition. But, in this case, items quantity and dispersion of usual food were simultaneously manipulated. In several other species, more information is available, as the number of food-associated calls increased with the divisibility level of the item discovered (house sparrows [2]; chimpanzees [22]) or with the quantity of food (rhesus monkeys [23]; chimpanzees [24]; spider monkeys [25]). The aim of the present study was to estimate the influence of different parameters related to feeding context in maternal domestic hens.

2. General material and methods

2.1. Animals and maintenance

All experiments were conducted with a total of 71 G11 strain maternal hens (Gauguet breeding). Each hen was housed with two chicks (IJA 657 strain) in individual wire mesh cages ($100 \times 70 \times 60$ cm) with opaque lateral partitions and nest boxes. Thus, each family group was visually, but not auditorily, isolated from the other groups. Birds were maintained under a constant artificial photoperiod (12L/12D). Temperature of the aviary was 20 ± 2 °C.

Animals were provided water and a mixture of whole wheat and commercial diet ad libitum.

2.2. Test procedure

The hens were tested with their chicks when the latter were 4–8 days old. Tests took place in a test-cage similar to the hen's home cage, except that the wire mesh floor was covered with a white plastic

sheet (experiments 1 and 3). Some tests were made in a circular arena (146 cm in diameter; 50-cm high) covered with blue linoleum (experiments 2 and 4). The test cages and arena were located in an experimental room ($230 \times 190 \times 285$ cm) separated from the aviary. A microphone was placed above the test area and connected to a stereo tape-recorder.

Each test lasted three minutes during which one or several food items were presented. Items were placed in either one or several transparent dishes fixed onto a small piece of wood.

The observer, placed behind a curtain with an observation window, counted the food calls. At the same time, the vocalizations were tape recorded and blindly counted again after each test.

More specific details are provided below for each experiment.

2.3. Statistical analysis

Non-parametric tests were used, especially Mann–Whitney U test and Friedman two-way analysis of variance by ranks, followed by further post hoc analysis using multiple comparison tests [26].

3. Experiments

3.1. Experiment 1. Influence of the quality of food items

In cockerels, some authors have demonstrated that food calling varies with the type of object available to the male [12,20]. They stressed that substantial amount of food calling was elicited by non-food items including feathers, dried faeces or wood shavings. In addition, males uttered food calling in the presence of non-food item significantly more often when the signal receiver was a strange female than when it was a familiar female. These authors suggested that the call refers to an object of the environment and is used in two different modes: honestly when food is present and deceptively when food is absent or of low palatability [27,28].

The aim of this experiment was to evaluate the effect of edible food and inedible items on maternal food calling.

3.1.1. Methods

Twenty maternal hens with their two chicks were tested in a test cage placed in an experimental room. Three different items were used: (1) worm/mash, five mealworms on 100 g of wet mash (50 g of pellets +50 g of water); (2) usual feed: 100 g of a mixture of whole wheat and commercial starter diet; (3) wood shavings: 5 g of shavings that represented the same volume as mixtures 1 and 2. Each item was placed in a transparent plastic dish (9 cm in diameter; 5 cm deep).

Before each test, the hens and their 4–6 d old chicks were placed in the empty test cage for a 5-min habituation period. The 3-min test began when a dish was introduced into the cage. During each test, only one type of item was placed in the dish. The order of presentation of the items was determined randomly over a 3-day period (one test per day and per hen).

3.1.2. Results and discussion

Maternal hens uttered food calls significantly more frequently in the presence of real food items than in the presence of inedible items (shavings) (Table 1). In the presence of shavings, only seven of the twenty hens emitted food calls, whereas nearly all hens uttered food calls in the presence of food (20 and 19, respectively, for worm/mash and usual feed).

When hens were in the presence of real food items, the quality of that food item modulated the emission of food calls: they uttered significantly more food calls in the presence of worm/mash than in the presence of usual feed (Table 1).

The mixture of mealworms and wet mash, eliciting the most food calls, is also known to be the hens' preferred food [16]. Thus, maternal hens utter these calls preferentially in the presence of food items rather than in the presence of inedible items and utter more calls in the presence of a preferred food item than in

Table 1
Mean (±SE) number of food calls uttered by maternal hens in the presence of edible or non-edible items

	Mean	SE	
Worm-mash	96.4	20.5	a
Usual feed	28.1	5.3	b
Shavings	7.8	3.7	c

Friedman test, $X_r^2 = 26.84$, $df = 2$, $p < 0.0001$. Within each line of data, pairs of means with different subscripts (a, b, c) differ significantly (multiple comparisons test, $p < 0.05$).

the presence of a less appreciated food item. These results agree with previous reports on domestic hens presented food items [16], on cockerels presented edible and inedible items [12,20], as well as on other species [1,29,30].

3.2. Experiment 2. Influence of experience with food type

In the previous experiment, we offered hens food types perceived as more or less palatable as they were all potentially edible and not repulsive. This experiment aimed to investigate how maternal hens reacted when the family group was presented with items that hens know to be repulsive.

3.2.1. Methods

Fifteen maternal hens were given a preliminary test in the absence of their chicks when the chicks were 2 days old. A dish (9 cm in diameter; 5 cm deep) containing 30 g of a mixture of wet mash, millet (white and yellow) and alpist seeds (one volume of pellets, for one volume of water and one volume of seeds) was placed in the centre of a circular arena (146 cm in diameter; 50 cm high). This preliminary test enabled us to form two homogenous sets of hens concerning food calling in the presence this food type. Set-A hens ($N = 7$) were given three successive 3-min training sessions, each with the same food type and in the same test arena, in the absence of their chicks when chicks were 3 days old (d3). A fourth identical training session was given the following morning (d4). Set-B hens ($N = 8$) were also given three training sessions on d3 and one on d4 in the absence of their chicks, but in this case 1% de quinine (0.3 g per ration) was added to the food. Set-B hens learnt during these four sessions that this food type was repulsive.

On d4, hens of both sets were given another 3-min test, but this time in the presence of their chicks, who do not know this food type. During this test, the observer recorded all food calls uttered by a hen and which element elicited the call (food or another item: dust or faeces). The number of 15-s periods during which the mother or her chicks pecked in the food dish was recorded. The hen's pecks directed towards parts of the arena other than the food dish and oriented towards other fragments were also recorded and named 'exploration'. The dish was weighed before and after the test to evaluate the quantity of food consumed by the family group.

3.2.2. Results and discussion

Set-B hens, which had learnt that the food was repulsive, uttered significantly less food calls than set-A hens, which had no negative experiment with the food (Mann–Whitney U-test, $p < 0.05$). This result is confirmed when we consider the total number of food calls uttered during a test or only the calls directed towards the food dish (Table 2). Moreover, set B hens pecked at the food significantly less often and explored more frequently than set-A hens (Mann–Whitney U-test, $p < 0.05$) (Table 3). Only set-B hens uttered some food calls in the presence of poorly identified elements (dust, faeces, irregularities in the floor covering). Nevertheless, the difference in the number of food calls uttered during exploration between the two sets of hens did not reach significance (Mann–Whitney U-test, $z = -1.74$, $p = 0.08$).

The chicks behaved like their mother: set-B chicks pecked less frequently at the food dish than did set-A chicks (Mann–Whitney U-test, $p < 0.05$) (Table 3). In addition, set-B family groups consumed significantly less food than did set-A family groups (Mann–Whitney U-test, $p < 0.05$) (Table 3).

The results of this experiment confirm that hens can learn the repulsive aspect of a food type [31,32]. Although the aversive aspect of the quinine used here was not sufficient to induce total loss of interest, it was sufficient to induce a drop in interest in the food and a clear decline in the tendency to utter food calls. This stresses that the tendency to utter food calls is strongly related to an animal's previous experience with that type of food.

The behaviour of set-B hens differed from that of set-A hens: they explored more the elements in their environment, although available manipulable elements were rare. Two hypotheses could explain this difference. First, the lack of interest in the quinine treated food could increase the hens' tendency to search for other centres of interest. On the other hand, maternal hens are able to modulate their behaviour in relation to that of their chicks [33,34] who are not yet neophobic [35] and could be attracted by the food presented. Their mother may then tend, by exploring the environment, to induce the chicks away from the food she knows to be bad.

Table 2
Mean (± SE) number of food calls uttered by maternal hens with a positive (set A) or negative (set B) experience with the food type

	Set A (positive experience)			Set B (negative experience)	
	Mean	SE		Mean	SE
Total	21.4	5.2	*	6.8	2.9
On food	21.4	5.2	*	3.4	2.2
Away from food	0			3.4	1.7

* Significant difference (Mann–Whitney U-test, $z = -2.10$ and $z = -2.87$, respectively, $p < 0.05$).

Table 3
Behaviour and ingestion of food by set A and set B animals

	Set A (positive experience)			Set B (negative experience)	
	Mean	SE		Mean	SE
Behaviour of hens					
Pecks (1)	8.4	1.2	*	3.0	1.2
Exploration (1)	0.6	0.3	*	5.8	1.1
Behaviour of chicks					
Pecks (1)	8.9	1.6	*	2.0	1.0
Ingestion by the family group (2)	1.8	0.7	*	0.2	0.1

(1) Mean number of 15-s periods when this behaviour was recorded.
(2) In grams.
* Significant difference (Mann–Whitney U-test, $z = -2.52$, $z = -2.72$, $z = -2.75$ and $z = -2.48$, respectively, $p < 0.05$).

3.3. Experiment 3. Influence of the quantity of food

The previous experiments stressed the importance of the qualitative aspects of food on food calling but other factors could also influence the food calling utterance. Indeed, the number of food-associated calls uttered by primates varies in relation with the quantity of food discovered by the caller [23–25]. This question has never been addressed in chickens. The aim of this study was to investigate whether, as in other species, the utterance of food calls by maternal hens is enhanced by the quantity of available food.

3.3.1. Methods

Twenty maternal hens with their 6 day-old chicks were tested in the experimental cage, as in experiment 1. To evaluate the effect of the quantity of food, we used a same food type (pellets for game birds) presented in two different quantities: 30 and 120 g.

During a 3-min choice test the two quantities of food were presented in two dishes (9 cm in diameter; 5 cm deep). One half of the hens were tested with the dish with the small quantity on the left and the dish with the large quantity on the right. The reverse positions were used for the other half of the hens.

The observer recorded all food calls uttered by a hen, which dish elicited each call, which dish elicited the first peck and whether the hens visited both food sources or not.

3.3.2. Results and discussion

The first choice was not influenced by the quantity of food in the dish (10 hens pecked first in the 30-g dish and 10 hens pecked first in the 120-g dish) and 75% of the hens pecked in both dishes during a test. Nevertheless, the number of food calls uttered differed in relation with the quantity of food. The hens uttered significantly more food calls when they found a large quantity of food in the dish than when there was less (respectively 24.4 ± 6.8 and 6.4 ± 2.4; Wilcoxon signed ranks test, $z = -2.20$, $p < 0.05$). This result agrees with reports on other species and those by van Kampen and Hogan [22] on cockerels, although in this case, the authors manipulated the quantity of mealworms (three versus one) as well as the disposition of the usual feed (in the trough or in the trough and spread over the floor).

3.4. Experiment 4. Influence of the dispersion of food sources

Several observations (Richard-Yris and Wauters, pers. obs.) on maternal hens in the presence of their chicks revealed that food calls were mainly uttered at the beginning of a feeding sequence, when hens discovered food. This is confirmed by the analysis of the number of food calls recorded during the 3-min tests in experiment 3. The number of food calls was significantly higher during the first minute of the test, when the hen discovered the food, than during the following minutes (respectively for the first, second and third minutes: 29.7 ± 6.5; 2.3 ± 1.6; 1.6 ± 1.6; multiple comparison test, $p < 0.05$). The question rises whether a fragmented food source would induce more food calls than a food source presented in bulk. In several species, the number of food associated calls increases with the degree of divisibility of the item discovered by the caller [2,36]. The aim of this experiment was to test the impact of a same quantity of a food type presented in bulk or in fragments on the production of food calls.

3.4.1. Methods

Sixteen maternal hens and their 5–6-day-old chicks were tested in a circular arena (146 cm in diameter) as in experiment 2. The food type tested was their usual feed. Two tests were made on two successive days. In test A, the food (400 g) was placed in one dish (20 cm in diameter; 5 cm deep). In test B, the 400 g of food were placed in five smaller dishes (9 cm in diameter; 5 cm deep; 80 g in each dish). Birds had to cover the same distance (63 cm) from the spot where they were placed at the beginning of the experiment to reach the first available dish (test B) or the single dish (test A). Half the subjects were given test B first, whereas the others were given test A first. The number of food calls directed towards each dish was recorded as well as the number of dishes visited in test B.

3.4.2. Results and discussion

Maternal hens uttered significantly more food calls in the presence of several sources of the same food, i.e., when food was dispersed ($X = 38.1 \pm 7.0$), than when there was only one large food source ($X = 24.6 \pm 4.8$) (Wilcoxon test, $z = -1.99$, $p < 0.05$). However, the interpretation of this result is not simple because the more frequently the hens changed feeding sites during a test, the more they uttered food calls (Spearman rank-order correlation coefficient, $r_s = +0.56$, $p = 0.03$). Three hypotheses could explain this result.

First, the possibility that five dishes with food are perceived by hens as more food than the same quantity of food placed in a single dish cannot be ruled out. This remark can apply to data for both chimpanzees [22] and house sparrows [2]. Second, the hens' exploratory tendency could be stimulated more by the presence of several food sources than by a single source. This relationship between a hen's predisposition to emit food calls and its tendency to explore its environment with its beak is illustrated by the positive correlation between the two factors when maternal hens with chicks were observed in the presence of an empty dish [34]. Finally, the result recorded in this experiment could be influenced by another factor. In situation B, chicks could potentially, at some times at least, be further from their mother than in situation A. Maternal hens are known to utter more food calls when their young wander off. The utterance of food calls then induces chicks to approach their mother [18,34].

4. General discussion

The experiments presented here show that food calling by maternal hens is influenced by many factors related either directly or indirectly to feeding context and underlined that the focus of communication as a vehicle for analysing complex cognitive processes is a good approach.

Some of the factors involved in the production of food calls by maternal hens can be compared to those reported by other authors concerning food calling by adult cockerels, but there are also discrepancies.

Adult cockerels [12], like maternal hens, uttered more food calls in the presence of real food than in the presence of inedible elements. Nevertheless, our data on maternal hens, compared to data recorded in quite similar conditions on cockerels, show that cockerels uttered more food calls in the presence of inedible objects than hens did. Indeed, van Kampen [37], van Kampen and Hogan [21] and Négrel (comm. pers.) reported frequent food calling by cockerels on shavings whereas maternal hens rarely uttered food calls in

this situation. Two hypotheses can be advanced. Males may probably be more sensitive to certain shapes or sizes of stimuli or, as suggested by Stokes [38], food calling may be more ritualised or symbolic in cockerels than in hens. On the other hand, maternal hens may be more sensitive than cockerels to the edible and palatable parameters of items. This last hypothesis could explain why hungry cockerels indiscriminately increase their food calling utterance in the presence of both edible and inedible items [21], whereas in maternal hens, hunger only increased the level of food calling in the presence of their usual feed, but not in the presence of their highly preferred food type, which always induces a high level of food calling [16].

The maternal hen's particular interest in edible and palatable items could find its origin in the fasting period they experiment during incubation. Nevertheless, the quantity of food consumed is not the only factor involved in food calling utterance. Indeed hens that stopped incubating without having chicks eat more and utter less food calls that maternal hens [39,40]. Nature and strength of social links seem to be involved in the food call production. This underlines the hypothesis of a multicausal induction of this call in males and females.

Mealworms always induce sustained food calling by cockerels as well as by maternal hens. This particular attractiveness can be explained by the shape and mobility of mealworms, but the possibility to manipulate the items could also be a very efficient stimulation. In addition, when a bird has access to mealworms, these worms could represent a fragmented food source that, we have seen above, potentially constitutes a more stimulating element for food calling than a more compact source.

The introduction of a visual novelty into the environment increases the tendency of cockerels to utter food calls. Novel stimulations from different sources (modification of the colour of part of the test arena, presence of a familiar female with unfamiliar adornment or an unfamiliar female) stimulate food calling by adult cockerels [21]. This result underlined that stimulation of their exploratory tendency plays a positive role in the production of food calls. The same type of phenomenon was observed in maternal hens when they were in the presence of a larger relatively unfamiliar environment [41] or were faced with a more complex structure of their feeding environment (experiment 4). However, it is difficult to know exactly whether the increase in food calling by maternal hens is only due to the increase in the mother's exploratory tendency or the consequence of a modification of the behaviour of her chicks, as we know that this also conditions food calling [16,18,34].

Even though, as we said above, the quality of the items presented undeniably plays an important role in food calling (experiment 1); this quality constitutes a characteristic which has been learned, at least in part, during the maternal hen's own experience (experiment 2).

It would be very interesting to compare our results with data for adult cockerels in so far as information on the existence of this phenomenon, like the possible impact of different quantities of available food (experiment 3) on the production of food calls currently lacks in the literature. Thus, in the case of adult cockerels, this fact prevent us from choosing between the assertions of some authors [21,38], who think that the nutritional function of food calls has become largely symbolic in males and that food calling of cockerels seems to facilitate sexual interactions and statements of other authors [11,42], who consider that the food call is really a food associated call.

Nevertheless, food calling by maternal hens clearly conveys the tendency of the mother to share items she recognizes to be edible in relation to her previous experience, as the quantity of food calls uttered varies in relation to the relative richness of the feeding context.

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