Cats reorganise their feeding behaviours when moving from ad libitum to restricted feeding

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Abstract

Objectives One identified solution to prevent obesity in cats is to control and limit their calorie intake. The objective of the present work was to better elucidate the impact of calorie cut-off on the feeding behaviour of cats.

Methods A control (n = 31) and a test group of cats (n = 38) were included in the present study. Both groups received the same food variety during the study. A period of ad libitum feeding was initially set (T0), followed by a 9-month mild calorie restriction period for the test group only (T9; average calorie restriction = 6%), and a final period of ad libitum feeding (T10). The individual cat feeding behaviours were measured via an electronic feeding system, and agonistic interactions between cats during food anticipation via video observations. Generalised linear mixed models were fitted to compare all feeding parameters between periods by group. No statistical analyses could be performed on the agonistic interactions data owing to their structure.

Results The feeding behaviour of the control group remained stable during the entire study, while the test group showed fewer but larger meals taken at shorter time intervals and a faster eating rate in response to calorie restriction. The average total number of agonistic interactions per cat increased during the calorie cut-off period in the test group only. One month after returning to ad libitum feeding, all behaviours were largely restored to baseline values.

Conclusions and relevance Behavioural changes expressed by cats under calorie restriction can explain some of the difficulties obtaining cat owners’ compliance with dietary restriction, especially in multi-cat households. Feeding strategies should be utilised to help cats be less impulsive and maintain normal feeding patterns when moving away from ad libitum feeding.

Keywords: Feeding patterns; calorie restriction; obesity management; ad libitum feeding

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Thus, the objective of the present work was to better elucidate the impact of calorie cut-off on individual cat feeding behaviours, as well as on interactions between cats during food anticipation.

Materials and methods

Cats
Eighty domestic shorthair cats were assigned to two groups of 40 cats each, and were balanced for sex, age, weight and body condition score (BCS). Several cats were removed before the start of the study following a failure to adjust to their social group, and others had missing data owing to veterinary care that they needed during the study. Only cats with complete data were included in the analyses, resulting in final groups consisting of 31 cats in the control group (age 7.5 ± 4.1 years; weight 4.4 ± 0.8 kg; BCS 5.7 ± 0.8/9; 58% of BCS >5/9) and 38 cats in the test group (age 8.3 ± 4.0 years; weight 4.2 ± 0.9 kg; BCS 5.3 ± 0.8/9; 34% of BCS >5/9).

The cats were group housed in an enriched environment. They had controlled individual food access via an electronic feeding system and ad libitum water access. Each group was physically separated into two different rooms, resulting in a total of four rooms. The study protocol was approved by the French government (Préfecture de la Somme, authorization number B 80-021-007).

Treatment

Food
The control and test groups received exactly the same variety of standard commercial maintenance foods presented according to an identical schedule over the entire study. Each day, cats received wet food in the morning (first serving) and dry food for the rest of the day and overnight (second serving). They also very occasionally received treats.

Calorie cut-off
A calorie cut-off was applied to the test group only via an electronic feeding system for 9 months. Once cats in this group had consumed their permitted ration, they could no longer access the feeders. Individual rations were established to meet the cat’s maintenance energy requirement based on the following formula: maintenance calorific intake = 60 × body weight (kg) × allometric factor. Rations were adjusted monthly based on the cats’ last weight measured, in order to maintain their ideal body weight or trigger a progressive weight loss no greater than 2% of body weight per week. The resulting average calorie restriction applied to the overweight cats of the test group (BCS >5/9) was 6%, corresponding to a mild restriction.

The calorie cut-off was initially set up as a calorie allowance for the entire day. However, cats then rapidly switched their original spontaneous 30/70 calorie intake ratio from the first (ie, wet food) and second serving (ie, dry food) to having the majority of their calorie intake in the first serving (ie, 70/30). This led to reduced access to the dry food for the rest of the day and overnight. The calorie allowance method was thus changed so that cats were allowed a maximum of 50% of their daily energy allowance from the morning wet food.

Data collection periods
The feeding patterns and behaviour of both groups were assessed before the start of the treatment, 9 months after the start of the calorie restriction and, finally, 1 month after the end of the calorie restriction: reference test periods T0 (ad libitum), T + 9 months (T9; restriction) and T + 10 months (T10; ad libitum).

The foods offered during the reference test periods were always the same commercial diets offered and followed the same schedule. These included different wet products (n = 6), dry (n = 6) and treat products (n = 2). Treats are not presented in the following results because the reference data were missing following a technical issue.

Recorded data
The BCS and body weight of each cat were measured monthly over the entire study, except during the final ad libitum period (T10) when weighing was done on a weekly basis. The BCS scoring was always done by the same trained person who was blind to the treatments of the cats.

The feeding patterns of the cats were automatically measured during each reference test period using an electronic feeding system (see the tables referred to in the ‘Results’ section for the complete list of feeding parameters recorded).

The agonistic interactions, including physical contact, as well as avoidance, were recorded during 3 mins of food anticipation before the first meal of the day (ie, wet food) based on videos. Two days of video were collected for each group and each reference test period.

Statistical analyses
Generalised linear mixed models were fitted to account for the correlated data (ie, the same cat participated in the test multiple times) to compare all feeding parameters between periods by group. A linear mixed model was also used to assess the weight evolution of the cats, treating time as continuous and including the time–BCS category interaction. No statistical analyses could be performed on the agonistic interactions data owing to the data structure. P values <0.05 were considered to be significant, and as showing a trend if they were between 0.05 and 0.1. All statistical analyses were performed in R 3.5.2\(^{25}\) and SAS 9.4 (SAS Institute).

Results of feeding patterns and agonistic interactions are presented for the test group as a whole. Indeed, non-overweight cats of the test group showed significant changes in their feeding patterns between T0 and T9 in
response to the end of ad libitum feeding that were similar to those seen in overweight calorie-restricted cats.

**Results**

**Weight and BCS**

Weight loss was considered as the relative weight loss, which is the percentage of weight loss relative to the original T0 weight. Overweight cats (BCS >5/9) in the test group significantly lost weight over the 9 months study duration while those in the control group did not (Table 1).

After 1 month of having returned to ad libitum food access, the average weight of the cats in the test group stabilised back to its initial value: 4.2 kg at T0, 4.0 kg at T9 and 4.2 kg at T10.

The percentage of overweight cats (BCS >5/9) in the test group was lower than the initial value after the 9-month calorie cut-off period and also after 1 month of having returned to ad libitum food access: 34% at T0, 11% at T9 and 13% at T10.

The weight of the test group cats at T10 was similar to T0, but there were fewer overweight cats. This partly resulted from some initially non-overweight cats putting on weight during the study without increasing BCS, and some initially overweight cats becoming non-overweight at T9 but regaining some weight at T10 without changing BCS category.

**Feeding patterns**

No significant change was observed in the feeding patterns of the cats in the control group over the study period for any food type. The feeding patterns of the cats in the test group were affected by the calorie cut-off period for both wet (Table 2) and dry products (Table 3).

When consuming wet products, cats in the test group displayed fewer (statistical trend) but larger and longer meals (including the first meal). An overall increased consumption was observed, as well as a faster intake (first meal and overall) and a shorter interval between meals (between the first and second meal, and on average).

When consuming dry products, cats in the test group consumed, on average, significantly fewer meals and had a lower overall intake. However, they started their first meal sooner, had larger meals and a faster intake (first meal and overall for both). The interval between meals also decreased (between the first and second meal, and on average).

One month after the end of the calorie cut-off period, the feeding patterns of the cats in the test group reverted to levels close to their initial T0 behaviours (Table 4). The

| Table 1 | Evolution of the weight of originally overweight cats (body condition score [BCS] >5/9) for the control and test groups over the calorie cut-off period |
|---------|----------------------------------------------------------------------------------------------------------------------------------|
| BCS category | Weight/month (%) | g/day | SEM | Df | t ratio | P value |
| Overweight control (n = 18) | 0.11 | 0.23 | 0.27 | 1308 | 0.86 | 0.39 |
| Overweight test (n = 13) | −0.95 | −1.35 | 0.32 | 1308 | −4.22 | <0.01 |
| Df = degrees of freedom |

| Table 2 | Evolution of the feeding patterns of the control and test groups with wet food between T0, when there was no calorie restriction for any group, and the end of the calorie cut-off period for the test group (T + 9 months [T9]) |
|---------|-------------------------------------------------------------------|
| Wet food feeding parameters | T0 | T9 | Evolution T0 to T9 |
| | Control | Test | Control | Test | Control | Test |
| Total number of meals | 3 | 3 | 3 | 2 | NS | \(\uparrow\) t |
| Total consumption (g) | 94 | 92 | 95 | 133 | NS | |
| Total consumption duration (mins) | 8 | 9 | 10 | 11 | NS | |
| Average meal duration (mins) | 3 | 4 | 3 | 6 | NS | |
| Average time between meals (mins) | 32 | 32 | 31 | 20 | NS | |
| Average eating rate (g/mins) | 12 | 10 | 11 | 14 | NS | |
| Average consumption per meal (g) | 38 | 39 | 35 | 84 | NS | |
| Latency to start the first meal (mins) | 4 | 3 | 3 | 1 | NS | |
| First meal total consumption (g) | 57 | 59 | 54 | 105 | NS | |
| First meal duration (mins) | 4 | 5 | 5 | 8 | NS | |
| First meal eating rate (g/mins) | 13 | 11 | 12 | 15 | NS | |
| Interval between first and second meals (mins) | 24 | 25 | 23 | 16 | NS | |

Bold arrow = significant evolution (\(P <0.05\)); non-bold arrow + t = statistical trend (0.05 \(\leqslant P \leqslant 0.1\)); NS = no significant evolution (\(P >0.1\))
Table 3  Evolution of the feeding patterns of the control and test groups with dry food between T0, when there was no calorie restriction for any group, and the end of the calorie cut-off period for the test group (T + 9 months [T9])

| Dry food feeding parameters               | T0       | T9       | Evolution T0 to T9 |
|-------------------------------------------|----------|----------|--------------------|
|                                           | Control  | Test     | Control  | Test     | Control  | Test     |
| Total number of meals                     | 7        | 7        | 7        | 3        | NS       | ▼        |
| Total consumption (g)                     | 49       | 47       | 47       | 33       | NS       | ▼        |
| Total consumption duration (mins)         | 11       | 13       | 11       | 7        | NS       | NS       |
| Average meal duration (mins)              | 2        | 2        | 2        | 3        | NS       | NS       |
| Average time between meals (mins)         | 189      | 183      | 196      | 122      | NS       | ▼        |
| Average eating rate (g/mins)              | 5        | 5        | 4        | 6        | NS       | NS       |
| Average consumption per meal (g)          | 7        | 7        | 7        | 14       | NS       | ▼        |
| Latency to start the first meal (mins)    | 115      | 98       | 117      | 24       | NS       | ▼        |
| First meal total consumption (g)          | 8        | 8        | 8        | 18       | NS       | ▼        |
| First meal duration (mins)                | 2        | 2        | 2        | 3        | NS       | NS       |
| First meal eating rate (g/mins)           | 5        | 5        | 5        | 6        | NS       | NS       |
| Interval between first and second meals (mins) | 172     | 161      | 147      | 94       | NS       | ▼        |

Bold arrow = significant evolution (P < 0.05); NS = no significant evolution (P > 0.1)

Table 4  Comparison of the feeding patterns of the test group with wet and dry foods between the initial (T0) and final (T + 10 months [T10]) ad libitum periods of the study

| Feeding parameters               | Wet food | Dry food |
|----------------------------------|----------|----------|
|                                  | T0 | T10 | P value | T0 | T10 | P value |
| Total number of meals            | 3  | 3   | NS      | 7  | 7   | NS      |
| Total consumption (g)            | 92 | 85  | NS      | 47 | 54  | ▼        |
| Total consumption duration (mins)| 9  | 10  | NS      | 13 | 33  | ▼        |
| Average meal duration (mins)     | 4  | 4   | NS      | 2  | 5   | ▼        |
| Average time between meals (mins)| 32 | 30  | NS      | 183| 179 | NS       |
| Average eating rate (g/mins)     | 10 | 10  | NS      | 5  | 4   | ▼        |
| Average consumption per meal (g) | 39 | 36  | NS      | 7  | 7   | NS      |
| Latency to start the first meal (mins) | 3  | 3   | NS      | 98 | 76  | NS      |
| First meal total consumption (g) | 59 | 53  | NS      | 8  | 9   | NS      |
| First meal duration (mins)       | 5  | 6   | NS      | 2  | 6   | ▼        |
| First meal eating rate (g/mins)  | 11 | 11  | NS      | 5  | 5   | NS      |
| Interval between first and second meals (mins) | 25 | 25  | NS      | 161| 128 | ▼        |

Bold arrow = significant evolution (P < 0.05); NS = no significant evolution (P > 0.1)

Table 5  Average number of agonistic behaviours per cat in the 3 mins preceding the first meal of the day for the control and test groups over the study period: when there was no calorie restriction for any group (T0), at the end of the calorie cut-off period for the test group (T + 9 months [T9]) and 1 month after the end of the calorie cut-off (T + 10 months [T10])

|                  | T0       | T9       | T10  |
|------------------|----------|----------|------|
|                  | Control  | Test     | Control | Test | Control | Test |
| Avoidance        | 0.34     | 0.27     | 0.20   | 0.27 | 0.17    | 0.29 |
| Contact          | 0.17     | 0.27     | 0.13   | 0.39 | 0.04    | 0.19 |
| Total            | 0.51     | 0.54     | 0.33   | 0.66 | 0.21    | 0.48 |
only significant differences observed compared with the original behaviour levels were a longer intake duration (first meal, total and average) and a smaller time interval between the first and second meal, associated with a slower but larger overall consumption of dry foods.

**Agonistic interactions**
The average total number of agonistic interactions per cat increased during the calorie cut-off period and decreased once cats were back to ad libitum feeding (T10) in the test group only (Table 5). The increase was driven by a rise in physical contact while the frequency of avoidance events did not change.

**Discussion**

**Feeding patterns**
Restricting the calorie intake of cats led to dramatic changes in normal feeding behaviour, resulting in fewer and larger meals, a shorter interval between meals, as well as faster eating rates.

The vast majority of the measured behaviours reflecting the feeding patterns of the cats were significantly affected by the calorie cut-off for both the first (ie, wet food) and second (ie, dry food) serving of the day. In addition, the test group showed a switch in whether the greater calorie intake ratio came from the first or the second serving of the day, with the original T0 30/70 ratio changing to 70/30 a few weeks after the initial daily calorie cut-off was put in place, suggesting that the cats became more impulsive. The change then applied in the calorie cut-off method led to an average balanced ratio where test group cats consumed half of their calorie intake from the first serving of the day (ie, wet food) and half from the second one (ie, dry food). This explains the observed increase in total consumption for wet food and decrease for dry food between the ad libitum T0 and restricted T9 periods.

The natural feeding pattern of the cats is an ad libitum meal patterning spread throughout the 24 h of the day, as described by several authors. The mild calorie cut-off applied in the present study resulted in cats coming to the bowl faster (for the second serving of the day only; ie, dry food), taking fewer but larger meals (that were also longer for wet food only) and eating much faster. This aligns with the behaviours observed in a previous study where cats’ access to food was restricted for 12 h, then to 8 h and then to 4 h, without decreasing the food quantity offered. If such a method did allow a reduction in the cats’ weight at the beginning, cats rapidly adjusted their behaviours and ended up consuming more food within the 4 h period than they had done in the 12 h period, showing that limiting the duration of food access led to overeating. In our study, the feeding patterns observed may be linked to an increase in food motivation/hunger when restricted. The longer meal duration could also be a strategy by the cats to stay at the feeder and avoid the risk of not having access again if they went out and came back later on.

Additional direct observation of the cats in the test group during the wet food meal showed that the faster eating rate was obvious for several of them, and resulted in bigger bites and less mastication than cats in the control group. Such feeding behaviour may affect the digestion process of the food, especially as the average meal size was at least twice as large in the test group as in the control group. This may also lead to nutritional/physiological impacts, but these were not measured.

One month after being back to ad libitum food access, the alteration of the feeding patterns were largely restored to baseline, showing that cats are able to readjust their behaviours back to normal after a calorie cut-off without long-term detrimental effects.

**Agonistic interactions**
Restricting the calorie intake of cats led to an increase in agonistic interactions (ie, fights) during meal anticipation vs their initial level in the test group; this was absent in the control group. The level of agonistic interactions in the test group went back to below its initial value once the cats were back to ad libitum feeding. Thus, the calorie cut-off likely resulted in cats in the test group being more food motivated, as also shown by the feeding patterns discussed previously, which created tensions and increased aggressiveness between individuals before the meal. This could result from frustration and relate to the ‘irritability aggression’ described by some authors. Such a relationship between food restriction and increased feeding motivation reflecting hunger and possible welfare impacts to have already been reported.

Agonistic interactions are known to possibly happen in cats around the food bowl. In our study, the increase of such occurrences was not associated with a subsequent increase in veterinary care. One may thus consider that the calorie cut-off used in this study did not have a significant detrimental effect on the cats’ physical welfare.

**Conclusions**
Taken altogether, the results of this study illustrate that even a mild dietary restriction can strongly affect cats’ feeding behaviours, including cat–cat interactions during food anticipation, and may account for some of the difficulties experienced when getting cat owners to comply with calorie restriction, especially in multi-cat households. In addition, it could be expected that the changes we observed in feeding behaviours would be associated with a greater occurrence of food begging in the home environment, especially at or near scheduled meal times, as suggested by the shorter latency to first meal observed.

Feeding strategies can be utilised to help cats maintain normal feeding patterns while on calorie restriction. Possible solutions include feeding cats separately in multi-cat households, dividing the total ration into...
multiple small meals over the course of the day (eg, with the use of automated feeders), using puzzle feeders that slow down eating while providing activity and stimulation, and offering foods that require more effort and thus take more time to be eaten.

The present data also indicate that nutritional strategies that rely less on calorie restriction (eg, foods favouring satiety) are of major importance for weight management.

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Ethical approval This work involved the use of experimental animals; or involved the use of non-experimental animal(s) (owned or unowned) outside of established internationally recognised high standards (‘best practice’) of individual veterinary clinical patient care. The study therefore had ethical approval from an established committee as stated in the manuscript.

Informed consent Informed consent (either verbal or written) was obtained from the owner or legal custodian of all animal(s) described in this work for the procedure(s) undertaken. No animals or humans are identifiable within this publication, and therefore additional informed consent for publication was not required.

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References
1 German AJ. The growing problem of obesity in dogs and cats. J Nutr 2006; 136: 1940S–1946S.
2 Chandler M, Cunningham S, Lund EM, et al. Obesity and associated comorbidities in people and companion animals: a one health perspective. J Comp Path 2017; 156: 296–309.
3 German AJ, Woods GRT, Holden SL, et al. Dangerous trends in pet obesity. Vet Rec 2018; 182: 25. DOI: 10.1136/vr.k2.
4 Ward E, German AJ and Churchill JA. The Global Pet Obesity Initiative position statement. https://static1.squarespace.com/static/597c71d3e58c621d06830e3f/t/5 da311c5519b6262c4dac512/1570968005938/Global+pet+obesity+initiative+position+statement.pdf (2018, accessed July 1, 2019).
5 Colliard L, Paragon BM, Lemuet B, et al. Prevalence and risk factors of obesity in an urban population of healthy cats. J Feline Med Surg 2009; 11: 135–140.
6 Corbee RJ. Obesity in show cats. J Anim Physiol Anim Nutr 2014; 98: 1075–1080.
7 Rowe EC, Browne WJ, Casey RA, et al. Early-life risk factors identified for owner-reported feline overweight and obesity at around two years of age. Prev Vet Med 2017; 143: 39–48.
8 Öhlund M, Palmgren M and Holst BM. Overweight in adult cats: a cross-sectional study. Acta Vet Scand 2018; 60: 5. DOI: 10.1186/s13028-018-0359-7.
9 Mars. New survey weighs up potential reasons behind the pet obesity crisis. https://www.bettercitiesforpets.com/resource/survey-weighs-pet-obesity-crisis/ (2018, accessed July 1, 2019).
10 Association for Pet Obesity Prevention. U.S. pet obesity steadily increases, owners and veterinarians share views on pet food. https://static1.squarespace.com/static/597c71d3e58c621d06830e3f/t/5ad75099aa4994bd7214ac2/152406315077/APOP+Press+Release+2017+Survey+with+Infographics.pdf (2017, accessed July 1, 2019).
11 O’Connell EM, Williams M, Holden SL, et al. Factors associated with overweight cats successfully completing a diet-based weight loss programme: an observational study. BMC Vet Res 2018; 14: 397. DOI: 10.1186/s12917-018-1740-5.
12 R Core Team. R: a language and environment for statistical computing. https://www.R-project.org/ (2018, accessed January 14, 2020).
13 Bradshaw JWS. The evolutionary basis for the feeding behavior of domestic dogs (Canis familiaris) and cats (Felis catus). J Nutr 2006; 136: 1927S–1931S.
14 Thorne CJ. Cat feeding behavior. Pedigree Digest 1985; 12.
15 Michel KE, Bader A, Shoter FS, et al. Impact of time-limited feeding and dietary carbohydrate content on weight loss in group-housed cats. J Feline Med Surg 2005; 7: 349–355.
16 D’Eath RB, Tolka, Björklund B, Kytzakaz I, et al. ‘Freedom from hunger’ and preventing obesity: the animal welfare implications of reducing food quantity or quality. Anim Behav 2009; 77: 275–288.
17 Moesta A and Crowell-Davis S. Intercat aggression – general considerations, prevention and treatment. Tierarztl Prax Ausg K Kleintiere Heimtiere 2011; 39: 97–104.
18 Beaver BV. Fractious cats and feline aggression. J Feline Med Surg 2004; 6: 13–18.
19 Knowles RJ, Curtis TM and Crowell-Davis SL. Correlation of dominance as determined by agonistic interactions with feeding order in cats. Am J Vet Res 2004; 65: 1548–1556.