Wildlife feeding activities induce papillae proliferation in the rumen of fallow deer

Deirdre McLaughlin · Laura L. Griffin · Simone Ciuti · Gavin Stewart

Received: 18 December 2021 / Accepted: 26 July 2022 / Published online: 26 August 2022
© The Author(s) 2022

Abstract
Wildlife feeding activities are growing as a trend in recent years, with wild ruminants (e.g. deer in urban parks) receiving an increasingly unnatural diet as a result of public attention. The effects of diet on the gastrointestinal tract of ruminants have been established in the context of animal agriculture, with highly modified diets driving morphological changes in the rumen papillae. However, these dietary effects have not been widely explored in wild ruminants that are exposed to recreational feeding. The aim of this study was to investigate the effects of human-wildlife feeding interactions on the rumen papillae of a wild population of fallow deer in Phoenix Park, Dublin. The length, width, and density of the ventral rumen papillae were compared across a variety of feeding behaviours, ranging from deer that consistently accept food from humans to deer that rarely, if ever, accept food from humans. The surface enlargement factor (SEF) was also calculated as a measure of overall absorptive surface in the rumen and was similarly compared. Statistical analysis revealed that consistent acceptors of food had significantly higher papillae density than those that do not accept food. Increased papillae density in deer receiving high amounts of human food suggests a shift in the internal rumen environment. A lack of significant change in the SEF suggests that a cellular change may be occurring. This artificial rumen state requires further attention to elucidate the full extent of these feeding impacts on the gastrointestinal integrity of these wild deer. Moreover, this is a call for research into other human-wildlife feeding interactions that occur in human-dominated landscapes, beyond the deer of Phoenix Park.

Keywords Fallow deer · Dama dama · Rumen · Papillae · Diet · Human-wildlife feeding

Introduction
In this age of urbanisation, there is a growing desire among the public to reconnect with the natural world. The feeding of wild animals, and in particular large, charismatic mammal species, is an increasingly popular activity driven by the desire for close encounters with wildlife. The intentional, long-term feeding of wildlife is known to have impacts on animal behaviour and population levels (Orams 2002). However, the physiological impacts of a human-modified diet on wild animals are largely unknown. Wild ruminants, like deer, are a popular target species for feeding activities, and their unique gastrointestinal tract makes them an interesting subject for unravelling the physiological implications of these interactions.

As a ruminant, the deer’s gastrointestinal tract is adapted to process high quantities of fibrous plant material. The rumen hosts a population of symbiotic cellulolytic microbes that ferment plant material and produce volatile fatty acids (VFAs) (Dijkstra 1994). VFAs are passed from the rumen to the bloodstream via the papillated rumen epithelium and are a major source of metabolic energy for the deer. The papillae are therefore important regulators of the rumen environment; their absorption and metabolism of VFAs help maintain a suitable pH for resident microbes (Ruckebusch and Thivend 2012).

Diet variation influences fermentation activity, VFA production, and papillae development. The associated effects on rumen development have been extensively researched in the context of animal agriculture, with a rapidly fermentable, energy-rich diet having marked effects on the rumen papillae. Brownlee (1956) pioneered this subject by demonstrating that less fibrous foods stimulate papillae growth in cattle.
An increase in papillae length on energy-rich diets has since been consistently documented in cattle (Harrison et al. 1960; Tamate et al. 1962), sheep (Xu et al. 2018), and goats (Shen et al. 2004). Papillae width has seen a similar effect, although less pronounced (Dirksen et al. 1985; Shen et al. 2004). Papillae proliferation in terms of increased density has been observed in some cases (Rickard and Ternouth 1965; Stobo et al. 1966), and absent in others (Xu et al. 2018). Lesmeister et al. (2004) suggested that papillae length exhibits greatest sensitivity to dietary treatments.

However, the scope of these dietary studies is limited to ruminant livestock in highly controlled environments. Studies on free-ranging ruminants have noted that selective breeding and artificial diets have resulted in substantial differences in the digestive physiology of wild and domestic ruminants (Clauss et al. 2010). Papillae morphology of wild ruminants responds to seasonal changes in forage quality and availability (Hofmann and Nygren 1992). Papillae length and width have been shown to vary seasonally in wild white-tailed deer and mule deer, while density is more likely to vary with feeding strategy (Zimmerman et al. 2006). The surface enlargement factor (SEF) is often used as a measure of mucosal absorptive area of the rumen due to the papillae. A study on free-ranging white-tailed deer fed a standard or low energy diet had variable effects on ruminal papillation; SEF decreased in females on a low energy diet, but did not decrease in males (Spilinek et al. 2020). There has been intrigue about the potential effects of an artificial diet in wild ruminants, but the subject has remained largely unexplored.

The wild fallow deer (Dama dama) population at Phoenix Park—Ireland’s largest urban park—presents a unique opportunity to broach this subject while also exploring the physiological impacts of human-wildlife feeding activities. Phoenix Park is home to approximately 600 wild fallow deer, over 80% of which are tagged annually at birth and are part of ongoing long-term longitudinal studies. Although prohibited, the feeding of these wild deer by park visitors is on the rise (Fig. 1) (Griffin et al. 2022a, b). This species’ natural diet consists primarily of grass, supplemented by leaves and seeds (Chapman and Chapman 1997). However, deer fed by visitors supplement their diet with unnatural food items that are energy-rich and readily fermented (e.g. bread, carrots, apples, biscuits, chocolate) (Griffin et al. 2022b). This unregulated feeding has raised concerns for the health and welfare of the deer. The aim of this study was to assess the effects of artificial feeding on the rumen papillae of the deer with insight from the voluminous animal agriculture literature; based on the studies mentioned above, we a priori predicted a change in the papillae length of deer that consistently accept food from park visitors when compared to those that only do so occasionally or rarely. We also investigated for the first time whether deer accepting food differed in papillae width, density, and SEF as a function of food acceptance from the public.

### Methods

#### Study area and population

The feeding observations for this study were conducted in Phoenix Park, Dublin, Ireland. Phoenix Park is a 707-ha urban park fully enclosed by the capital city and is inhabited by a historic population of approximately 600 fallow deer. These wild deer are confined to the natural areas within the park walls due to being city-locked with no opportunity for emigration or immigration. The deer feed on grass, leaves, and seeds that are naturally abundant in the park. Adult deer in this population are devoid of natural predators; only new-born fawns are at risk of occasional predation by red foxes. Due to few top down influences, annual culling of the population is carried out by professionals and is managed by the Office of Public Works, thus making rumen samples available for this study. These deer have been documented by University College Dublin wildlife biologists since the 1980s. The yearly ear-tagging of new-born fawns has led
to over 80% of the population being identifiable for further research.

The natural appeal of Phoenix Park and its wild deer population is recognised by 10 million annual visitors. As a result, these deer experience long-term exposure to humans. In the past 10 years, there has been an increase in wildlife feeding activities wherein park visitors approach the deer at close proximity in order to feed them unnatural food items. This has led to the development of different feeding behaviours among the deer. These feeding interactions were observed passively and documented at a distance deemed safe and non-invasive (Griffin et al. 2022b).

**Observational data and description of feeding behaviour**

Observational data regarding the feeding behaviour of individuals was collected during the summer months from 2019 to 2021, encompassing the majority of the tagged population and modelled accordingly (Griffin et al. 2022b). The feeding behaviour of individuals was described as a continuum of willingness to interact with humans for food (i.e. feeding rank), ranging from high-scoring individuals that consistently seek and obtain food to low-scoring individuals that avoid human contact and do not receive food (Online Resource 1). Observations were also made on the types of food offered by visitors during feeding interactions, with over 9500 food item observations collected (Griffin et al. 2022b). Human food offered included carrots, bread, apples, and junk foods (i.e. biscuits, chocolate, and crisps). Some deer consistently seek these food items from visitors while others only do so occasionally or not at all. This variation in feeding behaviour occurs inter-individually; food-seeking deer coexist alongside their food-shy counterparts. Herds are composed of multiple behavioural types; these feeding habits are uniquely behavioural and are not influenced by locational variance in diet. Therefore, deer receive vastly different diets based on their willingness to ‘beg’ for food, with some receiving a more human-modified diet than others (Griffin et al. 2022b).

**Sample collection**

Deer rumen samples were obtained from the annual culls at Phoenix Park, Dublin. The culls were performed during November or January from 2019 to 2021. Individual deer were culled at random. This study consisted of 71 deer. Each culled deer was identified using the aforementioned unique colour-number combination ear-tags. The feeding rank associated with that tagged individual was extracted from a previously established database (Griffin et al. 2022b). Due to the non-selective nature of the cull, this study consisted of 33 females and 38 males, ranging in age from 1 to 14 years old. From this dataset, 10 were obtained from January culls and 61 were obtained from November culls. Across the 3 years of sampling, 16 were collected from 2019, 18 from 2020, and 37 from 2021.

**Papillae measurements**

The rumen mucosa of each deer was assessed for papillae length, width, and density. The ventral region was chosen as the site of biopsy due to its high blood flow and, therefore, high absorption capacity (Von Engelhardt and Hales 1977). For each of the 71 sampled deer, a 1-cm² section was cut from the ventral region of the rumen. Papillae length and width were measured in millimetres with a ruler and were determined by calculating the mean of three randomly selected papillae. Papillae density per square centimetre was determined by calculating the mean of three individual counts. The SEF was calculated to describe the absorptive surface area of the rumen subsample (Hofmann and Nygren 1992). The SEF was calculated as follows:

\[
\text{SEF} = \frac{(2 \times \text{papillae surface}) \times \text{papillae density} + \text{base surface}}{\text{base surface}}
\]

Papillae surface was the product of length and width, and base surface was the sample area.

**Statistical analysis**

Analyses were conducted in R 4.0.3 (R Core Team 2020). The dataset consisted of 71 rows, with each representing an individual deer with associated information (response variables) on papillae length, width, density, and SEF. Moreover, each deer was associated to several predictors, namely feeding rank, sex, age, month (2 levels January, November) and year (3 levels 2019, 2020, or 2021) when the sample was collected. All the predictors were categorical with the exception of age which was expressed as years old, and feeding rank which was described on a scale ranging between 3 (does not accept food) and 4 (consistently accepts food). Prior to model fitting, we screened the predictor variables to exclude any collinearity issues; categorical predictors were assigned a numerical value for the collinearity screening (Dormann et al. 2013).

We fit four linear regression models using the `lm` function (R Core Team 2020) with papillae length, width, density, and SEF as the response variable, respectively. Feeding rank, sex, age, month, and year were fitted as fixed effects for each model, with a quadratic effect being applied to age to account for possible non-linear patterns. We found that there was no significant effect of feeding rank on papillae length, width, or SEF, and so these models were excluded...
from further analysis (Online Resource 2). The remaining papillae density model is described as follows:

\[
\text{Papillae density} \sim \text{sex} + \text{age} + \text{age}^2 + \text{feeding rank} + \text{month} + \text{year}
\]

We screened the model residuals and successfully met the assumptions of linear models. We then plotted the desired effects using the \texttt{ggeffects} package (Lüdecke 2018) and extracted the model coefficients.

### Results

Papillae density was not significantly affected by sex or age of the individual, nor was it affected by month or year of sampling (Table 1). Papillae density was strongly influenced by feeding rank \((P = 0.018)\) \((\text{Table 1})\). The willingness to interact with humans for food correlates with papillae density \((\text{Fig. 2})\). Deer that consistently accept food had significantly higher papillae density \((53 \text{ papillae/cm}^2)\) than those that do not \((35 \text{ papillae/cm}^2)\) \((\text{Fig. 2})\).

### Discussion

Our findings reveal a physiological distinction between the wild deer that regularly accept food from people and those that do not. Our initial expectation that papillae length would be most indicative of the feeding behaviour of these deer was dismissed. Instead, papillae density was highly sensitive to feeding behaviour. We, therefore, theorise that an increase in papillae density is the most appropriate response for this sample population, where human food items are highly variable in quality, quantity, and availability.

Due to the regulatory role of the rumen papillae, their increase would suggest higher rates of fermentation, VFA production, and, therefore, declining ruminal pH. However, this histological change was not accompanied by an increase in absorptive surface in the rumen \((\text{Online Resource 2})\). The absorption of VFAs depends on papillae surface area and the availability of transport proteins \((\text{Penner et al. 2011})\). It is possible that these human-deer feeding interactions incur a cellular response. Cell adaptation in terms of transporter activity can occur without a corresponding change in absorptive surface area \((\text{Penner et al. 2011})\).

Deer that consistently accept human food are receiving a highly variable and, therefore, acidogenic diet \((\text{Bevans et al. 2005})\). Further research is necessary for understanding the full extent of the effects these recreational feeding activities have on wild ruminants. There are numerous avenues to investigate: VFA transport proteins, VFA composition, pH, and microbial community structure.

Wild populations present unique challenges for research. There are some limitations to consider for this study. Firstly, time constraints related to culling operations only allowed for the collection of tissue from the ventral region of the rumen. Papillae morphology and SEF do not respond uniformly to diet and have been shown to vary regionally within the rumen of fallow deer \((\text{Clauss et al. 2009})\). Ideally, multiple regions of the rumen \((\text{e.g., atrium ruminis, dorsal region, and caudal-dorsal blind sac})\) should be sampled to describe the effect of an artificial diet on papillae morphology of the whole rumen. Secondly,
culminating operations restricted this study to January and November. We suspect that human-deer feeding interactions are at their greatest intensity during the summer months when the weather is favourable, tourism is high, and families are more likely to visit (Griffin et al. 2022a). It would be preferable to have multiple sampling periods throughout the year to account for variance in feeding intensity and seasonal patterns.

There is a growing need to study natural wildlife populations in their increasingly unnatural state. Here, we have demonstrated the generation of an artificial rumen state as a consequence of popular human-deer feeding interactions. This is a brief glimpse into the physiological impacts of wild ruminant feeding activities—one that demands more attention in the interest of wildlife management and conservation. These unregulated feeding activities are not exclusive to the deer of Phoenix Park; they occur in numerous wild species across all human-dominated landscapes. It is important that the physiological effects of these interactions are investigated wherever possible. Further research here is key to characterising and evaluating the physiological effects of these human-wildlife interactions.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s13364-022-00647-1.

**Acknowledgements** We wish to thank the Office of Public Works for their support and members Paul McDonnell and Maurice Cleary for facilitating the collection.

**Author contribution** All authors contributed to the study conception and design. Collection of observational data was performed by LLG, rumen sample collection was performed by GS and SC, and analysis was performed by DML, LLG, and SC. The first draft of the manuscript was written by DML and edited by all authors who approved the final manuscript.

**Funding** Open Access funding provided by the IReL Consortium DML was partially funded by Crawford-Hayes bursary scheme. LLG and SC were supported by the Office of Public Works, grant #R19730.

**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author upon request.

**Code availability** The R scripts generated during the current study are available from the corresponding author upon request.

**Declarations**

**Ethics approval** Restricted, authorised culling of the Phoenix Park deer population is performed annually by Irish government bodies (Office of Public Works; National Parks & Wildlife Service) under strict national laws. To minimise the ethical impact of this study, ruminal tissue samples were only obtained from animals which had been already culled. Collection of animal behaviour observations was cleared by the Animal Research Ethics Committee, University College Dublin: care permit AREC-E-18–28-Ciuti.

**Conflict of interest** The authors declare no competing interests.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

**References**

Bevans DW, Beauchemin KA, Schwartzkopf-Genswein KS, McKinnon JJ, McAllister TA (2005) Effect of rapid or gradual grain adaptation on subacute acidosis and feed intake by feedlot cattle. J Anim Sci 83:1116–1132. https://doi.org/10.2527/2005. 8351110x

Brownlee A (1956) The development of rumen papillae in cattle fed on different diets. Br Vet J 112:369–375. https://doi.org/10.1016/ S0007-1935(17)46456-6

Chapman D, Chapman N (1997) Fallow deer: their history, distribution and biology. Machynlleth, Wales

Clausen M, Hofmann RR, Stickel J, Streich WJ, Hummel J (2009) The intraruminal papillation gradient in wild ruminants of different feeding types: implications for rumen physiology. J Morphol 270:929–942. https://doi.org/10.1002/jmor.10729

Clausen M, Humle ID, Hummel J (2010) Evolutionary adaptations of ruminants and their potential relevance for modern production systems. Animal 4:979–992. https://doi.org/10.1017/S1751731111 0000388

Dijkstra J (1994) Production and absorption of volatile fatty acids in the rumen. Livest Prod Sci 39:61–69. https://doi.org/10.1016/0301 6226(94)90154-6

Dirksen GU, Liebich HG, Mayer E (1985) Adaptive changes of the ruminal mucosa and their functional and clinical significance. Bov Pract 1:16–120. https://doi.org/10.21423/bovine-vol1985no2 p116-120

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Griffin LL, Haigh A, Conteddu K, Andaloc M, McDonnell P, Ciuti S (2022a) Reducing risky interactions: identifying barriers to the successful management of human–wildlife conflict in an urban parkland. People Nat. https://doi.org/10.1002/pan3.10338

Griffin LL, Haigh A, Amin B, Faull J, Norman J, Ciuti S (2022b) Artificial selection in human-wildlife feeding interactions. J Anim Ecol https://doi.org/10.1111/1365-2656.13771

Harrison RN, Warner RG, Sander ED, Loosli JK (1960) Changes in the tissue and volume of the stomachs of calves following the removal of dry feed or consumption of inert bulk. J Dairy Sci 43:1301–1312. https://doi.org/10.3168/jds.S0022-0302(60)00317-9

Hofmann RR, Nygren K (1992) Ruminal mucosa as indicator of nutritional status in wild and captive moose. Alces (Suppl.) 77–83. https://alcesjournal.org/index.php/alces/article/view/1781. Accessed 30 May 2022
