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Review Article

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The Effects of Diet on Anatomy, Physiology and Health in the Guinea Pig

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Abstract

Given the increasing popularity of the guinea pig as a pet it is, perhaps, surprising that relatively little is published as to their husbandry and dietary requirements. Indeed, a review of the literature currently available to owners, scientists and clinicians alike has found it to be scarce, highly variable and, at times, overtly contradictory. This review and data collection collates the husbandry and dietary information available and discusses the variable information available and the differing practices published in the literature in relation to the guinea pig. A questionnaire was also used to gather owner-reported data on feeding regimens from both the UK and Poland in order to better understand the range of feeding habits that owners employ. Despite the lack of information available in comparison with that available for other companion and livestock animals advances in knowledge are being made. With guinea pig numbers increasing in many countries and owners seeking husbandry and veterinary advice and interventions it is imperative that we understand guinea pig health and welfare issues. The data and review gives novel insights into how guinea pig husbandry affects health and welfare.

Keywords: Guinea-pig; Anatomy; Physiology; Diet; Nutrition; Health; Genetics

Background to the Guinea Pig

The domestic guinea pig, *Cavia porcellus,* also known colloquially as the 'cavy' belongs to the *Caviidae* family of rodents, originating from the grasslands and Andes Mountains of South America [1]. Following its domestication in 500-1000 AD, the guinea pig has been kept as an important source of food and is still eaten in many parts of South America today [2,3]. Since being introduced to Europe by Spanish colonialists in the 16th century, they have been commonly kept as pets, as well as used extensively in medical research with the first documented experiments performed on guinea pigs dating back to 1780 [1,4]. Since that time guinea pigs have played a pivotal role in epidemiological study and pharmaceutical development [1]. Their use in research has been declining rapidly since its peak in the 1960s, from around 2.5 million annually in the USA, to just over 200,000 in 2010 [5,6]. As the population of guinea pigs used in research declined, the popularity of the guinea pig as a pet has soared. In 2012 around 13,000 guinea pigs were being used in UK laboratories, yet approximately 1 million were being kept as pets in UK households, an equal number to that of rabbits [7,8]. Indeed the Pet Food Manufacturer's Association have reported the guinea pig as the UK's 7th most popular pet, kept in more households than any other pet rodent [8].

Anatomy and Physiology of the Guinea Pig

Although there is wide variability across the literature, it is generally believed that sow pups reach sexual maturity earlier than boars, with puberty reached at around six weeks in sows and nine to ten weeks in boars [9]. Upon reaching sexual maturity, females come into oestrus approximately every 16 days [10]. If breeding is desired, it is important to do so before the sow reaches six to seven months of age, to prevent the permanent fusion of the pubic symphysis and resultant dystocia [11]. Adult weight is reached at eight to 12 months of age, with boars weighing up to 1200 g and sows up to 900 g [2]. Despite reaching adult weight at this age, CT scanning has evidenced that bone growth and development are still occurring beyond 12 months [12]. Life expectancy varies broadly across the literature from two to eight years but is generally considered to be between around five or six years [13]. As a hystricomorph, or 'porcupine-like' rodent alongside chinchillas and degus, the guinea pig sow has a characteristically long gestation period of between 59 and 72 days, approximately double that of the rabbit, and gives birth to precocial young [2]. Litter size varies from two to six, with an average of three or four pups, each weighing between 60 and 120 g [1]. The young pups are born mobile, fully-furred, with their eyes open and teeth present, and are, therefore, able to consume solid food within a few hours, although will still suckle for two to three weeks [2,10].

The literature is divided as to how the circadian rhythm of guinea pigs can be classified [14]. Some authors have categorised guinea pigs as diurnal, being most active during daylight hours, whilst others have found them to show no circadian rhythm at all, instead having two to three hour periods of activity followed by a short period of rest [2,10,11,15]. Whilst this discord is seen across literature covering both domesticated pet guinea pigs and those used in research laboratories, it is generally agreed that wild guinea pigs tend to be crepuscular, with most activity seen at dawn and dusk [1,10]. It has also been found that the majority of behaviour of domesticated guinea pigs is similar to that of their wild counterparts [10]. In the wild, guinea pigs are sociable, rarely aggressive, vocal animals, living in groups of five to ten animals [16]. They have a good sense of sight and smell, although primarily use sound/language to communicate, being capable of producing up to 11 different vocalisations for specific situations [11,17]. However, their excellent hearing does mean that they are particularly sensitive to, and easily distressed by, loud or sudden noises, and tend to freeze in response [11]. In distinct contrast to other rodents, guinea pigs do not dig burrows or build nests [18]. Wild guinea pigs favour tunnels or nests made by other animals as well as the protection provided naturally by vegetation [19].

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Husbandry of the Guinea Pig

Due to the highly sociable nature of guinea pigs, most literature aimed at pet owners advises keeping guinea pigs in groups of at least two [2]. It has been established that keeping an animal with at least one other compatible individual significantly reduces stress in many species of mammals [20]. Despite the recognition that isolation can compromise an animal's welfare, scientific needs can justify laboratory guinea pigs being kept solitarily, in order that interaction between animals does not interfere with the research being carried out [10]. In such cases it is the needs of the research that lead housing and husbandry decisions, rather than simply the welfare of the animal [11]. As a result, laboratory-targeted literature should be referenced with caution by domestic owners and by the breeders and practitioners advising them. Traditionally guinea pigs and rabbits have been housed together, and up to even the late 1980s owners were advised that cohabiting guinea pigs and rabbits did not pose a problem [21]. However, it is now recognised both in the literature targeted at professionals and in advice aimed at lay owners that rabbits do not make suitable companions for guinea pigs. A number of concerns have been raised about housing the two species together, such as their different dietary requirements, the risk of stress to the guinea pig due to bullying, and the risk of injury due to the powerful kick of rabbits and potential attempts at mating [22,23]. Unsurprisingly it has been demonstrated that guinea pigs actively seek out fellow guinea pig company in preference to that of rabbits [24]. Additionally rabbits can carry subclinical *Bordetella bronchisepta* which can cause pneumonia in guinea pigs [11].

A solid-bottomed enclosure with dust-free bedding such as wood shavings or shredded paper is the preferred housing, as wire mesh cages can result in limb lacerations and fractures [11]. Pododermatitis (also known as bumble foot) can also result from the use of wire mesh cages, with the development of pressure sores as the bodyweight of the guinea pig is concentrated on to its relatively small feet [1]. Guinea pigs do not tolerate high temperatures or humidity well, and therefore an ambient temperature of around 21˚C, with draughts minimised should be maintained [11]. Environmental enrichment is important, in particular the provision of hiding spots such as large bore pipes that function as tunnels [9].

More recently the question of UVB light requirement in the guinea pig has been studied in order to ascertain whether there are any clinical or physiological complications linked to this practice or, indeed, whether it can improve their health. There were previously no recommendations for guinea pig owners in relation to the type of lighting that should be provided and whether too much, or too little, UVB caused lasting clinical complications, especially in animals kept inside. It was postulated that guinea pigs should be used to higher levels of UVB as in their native environment they are used to high altitudes, in addition UVB in most other vertebrates is utilized to create vitamin D but it was not known whether this was essential for guinea pigs [25]. In this study guinea pigs received either UVB supplement or no additional UVB and it was observed that 25 hydroxyvitamin D levels did differ, with higher values being seen in the treatment group (120 mmol/L to just under 80 mmol/L) in comparison to control animals (20 mmol/L to 40 mmol/L). Ionised calcium was significantly increased (1.52 mmol/L in controls and 1.58 mmol/L in supplemented animals, $p<0.0001$). The treatment group also had slightly thicker corneas than controls, but a number of other factors such as prevalence of ocular disorders, skin abnormalities and dental abnormalities, bone density, plasma parathyroid hormone, sodium, albumin and total blood protein levels were not altered between the groups [25]. The authors indicated that artificial UVB given to guinea pigs could be a good way to raise and maintain vitamin D levels but that longer term studies would be advisable. Guinea pigs do not respond well to change and enjoy a set daily routine [10]. In particular, they can become distressed following movement of housing or changes in food and water containers, and as such, must be slowly habituated to any changes [10,26].

Dietary Requirements of the Guinea Pig

The guinea pig is an obligate herbivorous hindgut fermenter and practises caecotrophy, consuming its own pellets [1,2,27]. This is to ensure maximal nutrient absorption from the caecal digesta, particularly vitamins K and B12 produced by the bacterial flora of the gut [24]. The guinea pig gastrointestinal tract is dominated by a large caecum which breaks down the cellulose content of the diet [28].

Dental care and diet

The hypsodont dentition of the guinea pig is designed to deal with large amounts of fibrous plant material with the open-rooted teeth erupting continuously throughout life [10,29]. It has been suggested that, if there is insufficient fibre in the diet, the teeth are not adequately worn down and severe malocclusions can occur, resulting in an inability to eat and starvation [2]. Therefore timothy or grass hay should make up the majority of the diet and be fed *ad libitum* [2]. Müller investigated the effect of different pelleted diets on incisor wear and tooth length in female juvenile guinea pigs (mean starting body mass 488 g ± 22 g, aged 9–11 weeks) [30]. Four different complete pelleted diets of increasing abrasiveness were tested, based on Lucerne, grass, grass with the addition of rice hulls and grass with the addition of rice hulls and sand respectively and a control of grass hay as a fifth diet. The study found a positive relationship between tooth growth and wear of upper and lower incisors in guinea pigs, indicating than in ever-growing teeth, the growth rate is regulated to compensate for wear, in common with a similar study on rabbits [31]. Contradictory to previous suggestions that internal abrasives cannot wear down tooth enamel or can only cause limited damage, the study indicates that internal abrasives do actually wear down teeth [32,33]. It was found that adding whole hay to the diet had a significant effect on tooth length of the upper incisors and cheek teeth but not the lower incisors or lower cheek teeth, and only dietary effects on wear and growth could be shown in the lower incisors [30,31]. Upper cheek tooth wear was highest using grass with the addition of rice hull and sand, and upper cheek teeth were affected more by abrasives than lower cheek teeth, with both of these characteristics similar to results in rabbits. This suggests that there is a similar mechanism of incisal gnawing and chewing in both species and suggest that feeding whole forages, while important when increased wear of incisors is aimed at, will not differ in the wear effect on cheek teeth when compared to high-fibre pellets. Tooth angle of cheek teeth differed significantly across diets, regardless of the diet abrasiveness, also adding to the suggestion that diet abrasiveness plays only a minor role in dental abnormalities observed in this species [30,31]. Therefore mineral imbalances or genetic predisposition may be a more likely cause of malocclusion and it should also be noted that these were not long term diet trials and only juveniles were investigated. The longest genetics study indicating that breeding may play a role on malocclusion was carried out in an inbred colony of strain-2 guinea pigs over four years. After each generation of breeding, future breeding stock were selected from animals which had siblings with no malocclusion problems noted and preferably no other close relatives affected [34]. The incidence of malocclusion was significantly reduced ($P<0.001$) by breeding from animals with no affected siblings, indicating that the malocclusion has a genetic basis at least in that strain.

Vitamin C

Another key dietary need of guinea pigs is that of vitamin C or ascorbic acid as, like humans, they lack the enzyme L-gulonolactone oxidase that is necessary to synthesise ascorbic acid from L-gulonolactone [28]. Hypovitaminosis C, also known as scurvy, usually presents following two to three weeks of insufficiency as lameness or pain due to intra-articular haemorrhage, anorexia, weight loss and general unthriftiness, progressing to death if left untreated [1,28,35]. Occasionally diarrhoea is also seen [11]. Sub-clinical scurvy presents as a generalised decrease in immune function, with increased incidence of bacterial pneumonia, acute enteritis and skin infections [28].

Guinea pigs need to consume 10 mg/kg of vitamin C daily, which can be achieved through a balanced diet (with many commercial guinea pig complete pellet diets containing plentiful vitamin C) or by adding to the drinking water [28]. Vitamin C degrades faster at higher temperatures, especially once 30°C is reached and a concentration dependent degradation is observed when added to water by between 20-50% depending on the dosage given [36,37]. Therefore although vitamin C can be relatively stable, it is suggested that water is changed every day in order to ensure an appropriate concentration for guinea pigs, but if well controlled, this could be extended. Shelf lives of pellets and vitamin C supplements must be adhered to Terril et al. [1]. Other good dietary sources of vitamin C include roots such as carrots and beetroot, and leafy greens such as kale, cabbage and dandelions, which also help to provide guinea pigs with environmental enrichment [2,28]. Since rabbits and other rodents can make their own vitamin C, it is not added to their pelleted feed and, therefore, rabbit and other rodent diets are unsuitable for guinea pigs [1]. Moreover, exclusively feeding a pelleted rat diet to a guinea pig can result in death due to vitamin C deficiency within 14 days [24]. It should be noted that breeding females require additional nutritional supplementation during pregnancy due to their two to three fold increase in vitamin C requirement and their inability to practise coprophagy as the abdomen expands [1,28]. Guinea pigs also require higher amounts of folic acid and lower amounts of vitamin D than rabbits and rodents and thus feeding guinea pigs rabbit or rodent food is likely to result in folic acid deficiency and hypervitaminosis D [9].

Macronutrients

Much work has been carried out by researchers and commercial feed companies in order to ascertain the appropriate levels of macronutrients within guinea pig diets. In addition to vitamin C there are a number of very important factors involved when designing an appropriate diet. Highlighted throughout the years has been the need for appropriate levels of n-6 fatty acids, especially in young males [38]. Using linoleic acid as the source of n-6 fatty acids, they concluded that although 0.24% of total calorific intake was sufficient for growth, 0.88-1.04 percent was optimum in reducing dermatitis levels. The protein content is also important and within that arginine has been shown to improve growth [39]. Tryptophan has also been shown to promote growth and prevent cataracts; the ideal requirement was 1.6-2.0 g/kg diet [40]. Other minimum amounts of amino acids to enable maximal growth and nitrogen retention, especially in young guinea pigs include crystalline L-amino acid 14.2 MJ ME/kg; lysine 8.4 g/kg; 5.4 g/kg each of phenylalanine and tyrosine; threonine, 5 g/kg; histidine, 3 g/kg; isoleucine, 5 g/kg; leucine, 9 g/kg; arginine 12 g/kg and valine 7 g/kg [41-49]. In relation to minerals 8 g calcium/kg and 4 g phosphorus/kg diet are suggested with low levels particularly affecting bones of younger animals [50,51]. Magnesium and potassium levels are dependent on the levels of both calcium and potassium but generally 1-4 g/kg of each is sufficient [52,53]. Many commercially available feeds are available specifically for guinea pigs based on the bulk of research carried out over the years, it should be noted that much research is also carried out by the commercial companies in addition to the peer reviewed works available. Guinea pig requirements often differ from those observed in other species such as rats and rabbits. It is essential that care should be taken when purchasing/developing a suitable guinea pig diet, especially in the young, pregnant and/or lactating animal.

Fruit and vegetables

The advice regarding whether or not fruit should be fed to guinea pigs is somewhat conflicting. In literature aimed at veterinary professionals, some authors state that no fruit whatsoever should be provided, as its sugar content is too high, whereas others maintain that the feeding of fruits such as kiwi and orange is appropriate [2,9,11]. Differences in advice directed at owners are also apparent, with some organisations advocating the feeding of small amounts of virtually all fruits, some advising unlimited feeding specifically of citrus fruits, whilst others declare that no citrus fruits should be given at all, with small quantities of apple being the only suitable fruit [54-56].

In order to understand the variability in feeding habits, owners in the UK and Poland completed an online questionnaire (under institutional ethical approval, n=197 respondents caring for 500 guinea pigs). Among the 84 Polish respondents, the English Short-haired and Abyssinian breeds were the most commonly kept, making up 43% and 30% respectively of the surveyed animals. In the British survey, the English Short-haired was again the most popular breed, making up 41.8% of the guinea pigs kept, with the Abyssinian being the second most popular breed, but making up just 15.6% of the cohort.

In the UK cohort there was a smaller proportion of owners that fed commercial guinea pig dry food, just 73.5% compared to 83% of Polish owners, with 3% of British owners feeding rabbit food and a further 3% feeding rodent muesli, neither of which meet the guinea pig's unique dietary requirements. The UK owners were also less likely to feed vegetables daily 77% in compared to 98% of Polish respondents ($P<0.0001$ chi-square). The frequencies which respondents fed their guinea pigs fruit and vegetables are shown in Table 1. Interestingly, the two guinea pigs that were being fed vegetables the least frequently the UK cohort (weekly and several times per month) were both showing signs of difficulty walking and bunny hopping, which are symptoms consistent with hypovitaminosis C.

Responses were even more variable on the subject of feeding fruit, which is perhaps not surprising given the disparity in advice available to owners in the literature and online. 99% of Polish owners did feed fruit, but on the whole, much less often than vegetables. Notably of the five animals within this cohort reported to have cataracts, four of them were fed fruit on a weekly basis, and may therefore have a diet higher in sugar and at greater risk of diabetes. 83.2% of UK owners surveyed feed their guinea pigs fruit which is fewer than the Polish owners, and with much greater variation in frequency ($P<0.0001$) (Table 1). Of the 264 UK guinea pigs that were fed fruit, eight had been diagnosed with cataracts (3.03%), whereas only one guinea pig out of the 133 not fed fruit (0.75%) had cataracts. Of those fed fruit, the highest proportion of cataracts (15%) was seen in the group that were given fruit several times per week. Greater sample sizes and further investigation into the glycaemic levels seen in guinea pigs with cataracts alongside their

Frequency of Feed/Country		Daily	Weekly	Fortnightly	Several times a month	Monthly	Never	NR
Poland n=84	Vegetables	82 (98%)	2 (2%)	0	0	0	0	0
	Fruit	52 (63%)	25 (30%)	3 (4%)	0 (0%)	2 (2%)	2 (1%)	1
UK n=113	Vegetables	69 (77%)	20 (22%)	0	1 (1%)	0	0	23
	Fruit	12 (11%)	40 (37%)	23 (21%)	5 (5%)	10 (9%)	18 (17%)	5

Table 1: Frequency with which Polish and UK owners feed their guinea pigs vegetables and fruit (n=84 and 113 respectively). Number and percentage (adjusted for non-respondents). NR denotes not responded to that question. Chi square showed significant differences in the numbers of people that fed their guinea pigs daily vs. weekly or less both vegetables P<0.0001 and fruit P<0.0001.

dietary history is now needed to determine how much of a risk factor fruit is for cataract development.

When looking at potential breed predispositions amongst the British cohort, the majority of cataracts were seen in the English Short-haired breed, with 3.4% of this breed being affected. Bone problems were also seen in the same percentage of English Short-haired animals. Bunny hopping was much more widely reported among the British cohort, recorded in 9.3% of English Short-haired, 11.4% of Abyssinian, 40% of Sheltie and 100% of the Satin breed guinea pigs. Intriguingly it is the Satin breed that has been most closely associated with the bone disorder osteodystrophia fibrosa, of which bunny-hopping could be a manifestation. It would be interesting to follow these cases up and undertake further investigations to see if they do indeed have this condition [57,58].

These data demonstrate the variation in feeding practices across guinea pig owners. This may be explained by the wide variety of advice available to owners, both in books, online and in the scientific literature. Additionally, finding information specifically on guinea pigs can be challenging as it is often amalgamated into that concerning other small mammals such as rabbits and hamsters. For example the management of fly strike in rabbits is often discussed in detail in the literature, but very little is available with regard to guinea pigs specifically [29].

Of greatest concern are the owners that are not feeding a guinea pig-specific dry food or not feeding vegetables regularly, as this advice seems to be quite consistent in the literature. Indeed some of the guinea pigs which were not receiving regular vegetables in their diet were described as displaying signs consistent with hypovitaminosis C. It is possible that the UK owners are probably following the latest advice in not feeding fruit as often as the Polish owners are, although since sugar content between fruits can be variable, without knowing the type of fruit being fed it is difficult to know how much sugar the animal is receiving.

Another study investigated the role of dietary sucrose and fat/cholesterol on the development of dyslipidemia and non-alcoholic fatty liver disease (NAFLD). Seventy 10 week old female guinea pigs were block randomised (on body weight) into 5 groups (n=14). After one week of acclimatisation they were each fed one of five diets. The control group were fed chow only and the other groups fed a chow based diet with either very high-sugar, high-fat, high-fat/high-sugar or high-fat/very high-sugar respectively [59]. Hepatic steatosis was found in most guinea pigs fed the high-fat diet but not in the control or very high-sugar diet group. This suggests that showed that feeding diets high in cholesterol and fat are the main contributing factors to dyslipidemia and NAFLD to non-alcoholic steatohepatitis (NASH) in guinea pigs.

Water and changes to diet

Their aversion to change can make guinea pigs very fastidious eaters, with the slightest alteration in diet resulting in a complete refusal to eat or drink [11]. Therefore any changes in diet, water supply or feeding receptacles should be introduced very gradually, for example, mixing a new bag of pellets with the old bag, rather than abruptly finishing one and then starting another [2].

One study investigated the water delivery system (open dish vs. nipple/bottle feeders) under differing dietary regimes. On all four diets, mean water intake was higher when a nipple drinker/water bottle was available. It was also important to note that water amount varied across diets (mean water consumption on hay diet from bowls=115.1 $g/kg^{0.75}$, nipple drinkers 120.6 $g/kg^{0.75}$. Parsley diet from bowls=30.1 $g/kg^{0.75}$, nipple drinkers=50.6 $g/kg^{0.75}$. Pellet diet bowls=101.8 $g/kg^{0.7}$, nipple drinkers at 138.0 $g/kg^{0.75}$. Seed mix diet bowls=63.6 $g/kg^{0.75}$, nipple drinkers=130.5 $g/kg^{0.75}$). Therefore diet and water delivery method affected water uptake, high dry matter diets and nipple drinkers increased mean water uptake [60].

Understanding water consumption is important clinically because a common problem in guinea pigs is uroliths or kidney stones, commonly composed of calcium carbonate [61]. The calcium component comes from excessive calcium in the diet which is filtered out in the kidneys. If insufficient water is consumed this leads to more concentrated urine sitting in the bladder and, therefore this, contributes to the formation of stones. Conversely more diluted urine dilutes the calcium carbonate making larger stones less likely to form, as has been suggested in rabbits [62]. This demonstrates the importance of the need for guinea pigs to drink a sufficient amount therefore it is clearly a husbandry issue if the water isn't provided in the manner that guinea pigs find best suits them.

Conclusions

Given the wide array of advice available to guinea pig owners, it is important that practitioners ensure they are up to date with the most current information when advising owners how to feed their animals. Of utmost importance is a balanced guinea pig-specific dry food, with *ad libitum* forage and daily provision of fresh vegetables rich in vitamin C. Seemingly fruit should be fed in moderation, perhaps just as an occasional treat, however if a sufficient diverse selection of fresh vegetables is available, then it may be best avoided entirely. It is also of note that much of the research into guinea pig diet is many decades old and whilst much work has been carried out in the commercial arena, little of the research has been published. This therefore highlights the potential for more research into guinea pig diet, husbandry and disease.

In order to minimise the propagation of genetic defects, the same common sense approach used in other species of not breeding from animals who have a congenital condition, or who have produced offspring with a congenital defect in the past should be employed. Further work is needed to fully understand the impact of diet on the development of conditions such as bone and ocular disorders in the guinea pig, and perhaps most importantly of all, to ensure that those findings are effectively communicated to owners so that they may act on them.

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