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Is gastrointestinal plasticity in king quail (Coturnix chinensis) elicited by diet-fibre or diet-energy dilution?

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Publication Details  
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Keywords
Quail, Coturnix chinensis, Phenotypic plasticity, Dietary fibre, Energy dilution, Digestive physiology, Gastrointestinal tract, Gastroliths, Gizzard

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Abstract

Phenotypic plasticity of organ size allows some animals to manage fluctuations of resource quality or availability. Here, we examined the phenotypic plasticity of the gastrointestinal tract of king quail (*Coturnix chinensis*) in a diet-fibre manipulation study. Quail were offered either a control low-fibre (high-quality) food (8.5% neutral-detergent fibre; NDF), or one of two experimental diets of higher fibre contents of 16% NDF (i.e. low quality food). To examine whether phenotypic plasticity of organ size was associated with the fibre content *per se*, or as a consequence of diluting the diet energy contents by adding fibre, one of the high-fibre feeds was ‘balanced’ with additional energy to match that of the low-fibre control diet. Total empty dry mass of the gastrointestinal tract was significantly heavier among birds offered the unbalanced high-fibre diet as compared with those offered the control diet, with birds offered the fibrous but energy-balanced diet having guts of intermediate size. The heavier entire-gut mass (dry) of quail offered the unbalanced high-fibre diet was associated...
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compensation to fibrous ingesta.

Keywords
Quail, *Coturnix chinensis*, phenotypic plasticity, dietary fibre, energy dilution, digestive
physiology, gastrointestinal tract, gastroliths, gizzard.
Introduction

Phenotypic plasticity of the avian gastrointestinal tract (gut) has been demonstrated for numerous species. For many avian herbivores the gut is especially responsive to changes in diet quality, but the physical and biochemical mechanisms that drive this plasticity are uncertain (Piersma and Lindstrom, 1997; Stark, 2005). Diet quality is important for vertebrate herbivores because they lack the ability to breakdown the hard-to-digest, fibrous components of vegetation aut-ezymatically (Barboza et al. 2009). Consequently, avian herbivores have been shown to increase the size of some intestinal organs, particularly the gizzard and paired caeca, to assist mechanical breakdown and the microbial-assisted fermentation of plant fibre that typically contain high proportions of cellulose, hemicellulose and lignin (Barboza et al. 2009). As such, a common method for investigating gut plasticity in herbivorous birds involves manipulating diet fibre levels by diluting high-quality, low-fibre feeds with increasing levels of hard-to-digest, fibrous material. In this regard, diet-dilution, and specifically diet-energy dilution, refers to the concomitant decrease in easily accessible nutrients (e.g. soluble cell contents) that accompanies any increase in the contents of hard-to-digest, fibrous material (i.e. digestible rather than gross energy contents – see Barboza et al 2009). However, to the best of our knowledge, no previous studies have been able to distinguish potential effects of diet-energy dilution from any effects associated with changes in food intake rates or as a consequence of any physical attributes that fibre might have on gut muscle. Therefore, using three novel diet formulations we isolated the effects of diet-fibre contents and energy dilution on the food intakes, metabolisability and gastrointestinal plasticity of a small herbivorous bird, the king quail (Coturnix chinensis).

The three diets offered to our quail (Table 1) were either a high-quality, low-fibre (LF) food containing around 8% neutral-detergent fibre (NDF; mainly cellulose, hemicellulose and
lignin) and around 3% acid detergent fibre (ADF; mainly cellulose and lignin), or one of two
high-fibre (low-quality) diets, each containing around 16% NDF and 6-7% ADF). To
examine whether changes in organ size were associated with the fibre content of the diets per
se, one of the high-fibre diets was balanced with additional energy (HFB) to match the energy
contents of the LF control diet, but the second high-fibre diet remained unbalanced (HFU),
and was therefore energy-dilute. Diets were same in all other respects (Table 1), and were
based on a standard poultry formulation (see methods).

Results and discussion
The first key finding of our study was that morphological adjustments of the quail gut could
be driven by energy-dilution effects, independent of food intakes and not solely as a
consequence of diet fibre. Specifically, quail offered the energy-dilute HFU diet had heavier
guts (entire dry mass) than those offered higher quality LF, but not the high fibre but nutrient
balanced (HFB) diets (Table 2). These differences were driven mainly by the significantly
heavier gizzards of the HFU-fed birds (wet and dry masses), being 1.4 times those of the LF-
fed quail and 1.2 times heavier than the HFB-fed birds, though the latter group’s gizzards
were not significantly different from either the LF- or HFU-fed birds. These results are
suggestive of a graded response in organ plasticity, whereby the need for a larger gizzard by
the HFB-fed birds was apparently tempered by access to more easily accessible energy
content of their diet.

Importantly, the larger gizzards of the HFU-fed birds apparently allowed them to maintain
body mass and body condition (fat mass) throughout the entire experiment (Table 3). By the
end of the experiment there were no significant differences in the abdominal fat masses
between the LF- or HF-fed quails (i.e. HFB or HFU; Table 2). Likewise, the HFU-fed quail
maintained feed intakes (dry and organic matter) comparable to those of LF-fed and HFB-fed birds (Table 1), in support of Starck’s (1999) suggestions that vertebrate gut-plasticity may be largely independent of food intake rates. Additionally, we provide the first experimental evidence that diet energy composition (or energy dilution) may be critically important for eliciting phenotypic plasticity of the vertebrate gut rather than the fibre content per se.

The second key finding of our study was that the HFU-fed quail had markedly higher metabolisability of plant fibres (NDF and ADF) compared with those offered the LF or nutrient-balanced HF diets (Table 3). Although the apparent metabolisability of organic matter by the LF-fed quail were on average higher than those by the HFB and HFU-fed birds, these differences were relatively minor compared with strikingly high levels of fibre digestion by the HFU-fed birds. Overall, the HFU-fed birds apparently metabolised 42% of ingested NDF, and 21% of ingested ADF, levels that were around twice those for the LF- and HFB-fed birds (Table 3).

The main sites for microbial-assisted fermentation in herbivorous birds are the paired caeca, and marked increases in caecal-mass have been observed in numerous bird species when feeding on high-fibre diets (e.g. Moss, 1974). However, the generally heavier paired-caeca of our HFU-fed quail was not statistically significantly different from that of the LF- or HFB-fed birds, although these data were quite variable (Table 2). Moreover, it is entirely possible that the differences in caecal masses for the HFU-fed birds were biologically relevant, particularly when other intestinal features are considered. For example, the HFU-fed birds tended also to have heavier proventriculus tissue (wet and dry masses; Table 2). The avian proventriculus is proximal to the gizzard (or ventriculus), and is the main acid-secreting organ, but there is evidence that increased acid digestion, along with greater mechanical
action in the gizzard, improves fibre degradation (Svihus, 2011). Moreover, mechanical
action of the avian gizzard is boosted by gastroliths (or gizzard rocks/stones), and these
tended to be more numerous \( (P = 0.06) \) and have a heavier overall mass \( (0.14) \) in the HFU-
fed birds (Additional Item Figure A1). It is also possible that changes to the caecal microbial
community-composition or population sizes could have affected higher fibre metabolisability
by the HFU-fed birds. Nonetheless, it is apparent that the high metabolisability of fibre by the
HFU-fed birds aided their maintenance of body-condition despite the challenging diet. As
such, we present tangible evidence for improved fibre digestion in an avian herbivore
associated with morphological plasticity of the gut.

Presumably, the larger gizzard of the HFU-fed quails facilitated mechanical and fermentative
digestion in our quail by improving fibre particle-size reduction, with the aid of gastroliths. In
this regard, food bulkiness may present an important mechanism activating phenotypic
changes of the vertebrate gut. Other studies have demonstrated that increases of structural
complexity of diets (i.e. increases in hard-to-digest fibre) increase the volume of gizzard
digesta, in addition to increases of gizzard tissue mass (Svihus, 2011). Larger particles are
generally retained in the avian gizzard until they are reduced below a threshold particle-size.
For example, in domestic chickens, particles typically pass from the gizzard only once they
are reduced to 0.5 -1.5mm (Moore, 1999). Such a threshold particle-size for passage from the
king quail gizzard is uncertain, but it is worth noting that our HFU-fed birds’ gizzards
contained 1.3 times the wet-contents of the LF-fed birds; the values being 5.7 ± 0.1 g and 4.3
± 0.1 g for HFU- and LF-fed birds respectively (Tukey’s HSD, \( P < 0.05 \)). Furthermore, the
HFB-fed birds’ gizzard masses (wet and dry; Table 2) and wet contents \( (4.6 ± 0.2 \) g) were
intermediate between the LF- and HFU-fed birds, suggesting that food bulk or particle size
had some effect on gizzard plasticity. Nonetheless, our central conclusion is that, in addition
to any textural, particle-size or fibre-bulk associated effects, phenotypic plasticity of the avian
gut can be elicited by the energy composition of the diet offered, or that of the subsequent
digesta and absorbta.

Methods and materials

Ethics

All experimental procedures were approved by the University of Wollongong’s Animal
Ethics Committee (Protocol No: AEI 1/15), in accordance with the Australian Code of
Practice for the Care and Use of Animals for Scientific Purposes.

Housing and animal management

Female king quail ($N = 18$ sexually mature, 2-3 year olds; *Coturnix chinensis*) were obtained
from a commercial supplier (Andrew’s Quail and Pet Palace, Smithfield, New South Wales,
Australia). All quail were held at the Ecological Research Centre (ERC) at the University of
Wollongong. Quails were housed individually in mesh-floored plastic cages (30 x 30 x 30
cm) and excreta were collected under each cage using a tray lined with non-stick baking
paper. Animal were housed in a temperature controlled facility (22°-24°C) at 50-60% relative
humidity and 14:10 h light:dark photoperiod (lights on at 0600h; full-spectrum UV
fluorescent bulbs). All quail were acclimated to housing and regular husbandry procedures
(e.g. handling and weighing, daily feed checks and changes, excreta collection) for three
weeks prior to experimentation. Quail were weighed ($\pm 0.1g$) every three days throughout
acclimation and experimental periods.
Feeding trials

All diets were prepared by The Poultry Research Foundation, The University of Sydney, Australia (Table 1). A standard low-fibre (LF) poultry feed contained 8.5% NDF (mainly hemicelluloses, cellulose and lignin) and 3% ADF (mainly cellulose and lignin) provided all animals with a consistent acclimation diet, and presented a control diet through the experimental period. Two additional diets were used during the experimental period, each containing higher fibre contents of 16-17% NDF and 6-7% ADF (Table 1). One of the high fibre diets was 'balanced' (i.e. high-fibre balanced; HFB) with corn oil to match the metabolisable energy contents of the LF diet (Table 1). The second high fibre diet was not energy-balanced and was therefore energy diluted, or 'unbalanced' (i.e. high-fibre unbalanced; HFU). Aside from differences in total fibre (NDF and acid-detergent fibre; ADF), diets were comparable in all other respects, particularly dry matter, organic matter and nitrogen contents (Table 1).

Following acclimation animals were randomly assigned to one of the three diets; LF (control), HFB or HFU. For those offered HFB or HFU, transition to the treatment diet occurred incrementally by diluting the LF diet with 50%, 70% and 100% of the treatment diet over three days, respectively. Once fully transitioned, quail remained on their respective diets for 14 days (N= 18 quail; n= 6 per treatment), during which daily feed intake (to ± 0.01 g).

Excreta were collected every three days on pre-weighed sections of non-stick baking paper (Castaway easy-bake; Packaging Direct, Wollongong). Samples of feed offered and complete excreta were frozen stored at -20°C.
Sample analyses

Samples of feed offered and excreta were thawed, thoroughly mixed and subsamples (ca. 1-2 g) from each quail bulked individually for the last nine days of the feeding trial. Bulked excreta and feed subsamples (ca. 1-2 g) were then oven-drying (forced convection) at 55°C until constant mass. Further subsamples (approximately 25% by weight) were dried at 103°C until constant mass to determine complete dry matter (DM). Dry feed and excreta were ground using a Wiley Mill (0.5 mm screen; Thomas Scientific, Wiley Mini Mill 3383-L40, Swedesboro, NJ, USA). Subsamples (ca. 0.5 g) of ground DM were ashed at 600°C for five hours in a muffle furnace (Model LCF15-12, LABEC Laboratory Equipment Pty Ltd, Marrickville, NSW) to determine organic matter (OM; i.e. DM-ash).

Fibre contents of feed and excreta were determined using an ANKOM Fibre Analyser (Model A220, ANKOM Technology Corp., Macedon, NY, USA). Subsamples (ca. 0.5 g) of feed and excreta dried at 55°C were analysed in duplicate for NDF and ADF content the sequential filter-bag technique. Prior to neutral-detergent digestion, samples were treated with 1 ml of heat-stable amylase (Sigma A – 3306; Sigma Aldrich, Sydney) for 80 min to remove starch, and sodium sulphite and decalin were omitted from the neutral-detergent procedure (Van Soest et al., 1991).

Subsamples of ground, dried (at 103°C) feed and excreta were analysed for gross energy content by combusting duplicate subsamples (0.5 g) in an automatic adiabatic bomb calorimeter (Gallenkamp, CBA-305, Gallenkamp and Co. Ltd, UK; calibrated every 15 samples using a benzoic acid standard), and total nitrogen content by combusting duplicate subsamples (200 ± 10 mg) using a Leco CNS-2000 combustion analyser (Leco Inc. St Joseph, Michigan, USA).
Food intake and apparent metabolisability

Apparent metabolisability (%) of diet components (e.g. dry matter, energy) was calculated as:

\[
\text{Metabolisability} = \frac{\text{Intake} - \text{Excreta}}{\text{Intake}} \times 100,
\]

where intake and excreta are in g day\(^{-1}\) and contents are per unit of DM or OM (Barboza et al. 2009).

Organ morphology

At the end of each feed trial period quail were euthanized by CO\(_2\)-asphyxiation followed by cervical dislocation and macroscopic dissections performed immediately. The gastrointestinal tract was removed and cleared of mesentery and fat. Organs (liver, crop, proventriculus, gizzard, small intestine, right and left caeca, and rectum-cloaca) were separated from the entire gut and weighed (±0.001g) prior to being emptied of contents, rinsed with physiological (0.9%) saline, and re-weighed to determine empty wet-mass. Organ lengths were measured using electronic calipers (precision 0.01mm). Gizzard contents were collected and stored frozen at -20°C for later analysis (contents of the gizzard for one animal from the HFU group was inadvertently discarded). Organs (excluding liver) liver dried (forced convection) to constant mass at 95°C.

Statistics

Values presented are means ± standard deviation (SD). We used an analysis of variance (ANOVA) to compare across diets. Assumptions for ANOVA were tested using the Ryan-Joiner test for normality and Bartlett’s test for homogeneity of variances. To meet the assumptions for ANOVA some data were log-transformed (ADF intake, gizzard dry mass), and all proportional data were arcsine transformed. Some data sets could not be transformed
to meet ANOVA assumptions (caecal wet mass, and entire-gut dry mass) and non-parametric
Kruskal-Wallace tests were in these cases. Significant differences detected by ANOVA or
Kruskal-Wallace ($P \leq 0.05$) were further explored using a Tukey's Honest Significant
Difference (HSD) post hoc tests. We used $z$-tests to determine whether there were significant
changes in quail body mass (as a proportion of initial mass compared with a hypothetical
change of zero). All analyses were performed using Minitab for Windows (version 15.1.30.0;
Minitab Australia).

Acknowledgements

All experimental procedures were carried out under approval from the University of
Wollongong Animal Ethics Committee (AE11/15), in accordance with the Australian Code of
Practice for the Care and Use of Animals for Scientific Purposes. Thanks to Aaron Cowieson
and Joy Gill (Poultry Research Foundation, University of Sydney) for diet formulations,
Professor Mike Thompson (School of Biological Sciences, University of Sydney) and
William Foley (Research School of Biology, Australian National University) for access to
facilities and assistance with analysis of samples. Sincere thanks to Tobias Wang and an
anonymous reviewer for their insightful and helpful comments and reviews, it is much
appreciated.

Competing interests

The authors declare no competing interests.

Contributions

AM, SW and SKCJ devised the experiment, SW and SKCJ performed the experiment, SW
performed sample preparation and analysis, SW and AM analysed the data, and AM and SW
wrote the manuscript.
Funding

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REFERENCES


Tables

Table 1: Formulations and contents for the low fibre (LF), high fibre balanced (HFB) and the high fibre unbalanced (nutrient diluted; HFU) offered to king quail.

<table>
<thead>
<tr>
<th>Contents as fed (%)</th>
<th>LF</th>
<th>HFB</th>
<th>HFU</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wheat – feed</td>
<td>72.5</td>
<td>44.6</td>
<td>54.4</td>
</tr>
<tr>
<td>Soybean meal</td>
<td>15.2</td>
<td>13.2</td>
<td>11.4</td>
</tr>
<tr>
<td>Wheat – bran</td>
<td>-</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td>Corn oil</td>
<td>2.1</td>
<td>7.1</td>
<td>1.6</td>
</tr>
<tr>
<td>Salt</td>
<td>0.14</td>
<td>0.17</td>
<td>0.11</td>
</tr>
<tr>
<td>Sodium bicarbonate</td>
<td>0.21</td>
<td>0.17</td>
<td>0.16</td>
</tr>
<tr>
<td>DL Methionine</td>
<td>0.08</td>
<td>0.08</td>
<td>0.06</td>
</tr>
<tr>
<td>Lysine HCl</td>
<td>0.02</td>
<td>-</td>
<td>0.02</td>
</tr>
<tr>
<td>Limestone</td>
<td>8.8</td>
<td>8.8</td>
<td>6.6</td>
</tr>
<tr>
<td>Dicalcium phosphate</td>
<td>0.77</td>
<td>0.77</td>
<td>0.58</td>
</tr>
<tr>
<td>Vitamin premix</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Composition (mean ± SD)</th>
<th>LF</th>
<th>HFB</th>
<th>HFU</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry matter (DM; %)</td>
<td>92.1 ± 0.2</td>
<td>92.0 ± 0.3</td>
<td>92.3 ± 0.3</td>
</tr>
<tr>
<td>Organic matter (OM; %)</td>
<td>85.5 ± 0.2</td>
<td>81.7 ± 0.3</td>
<td>85.2 ± 0.2</td>
</tr>
<tr>
<td>Gross energy (kJ g⁻¹ OM)</td>
<td>16.4 ± 0.2</td>
<td>18.5 ± 0.8</td>
<td>17.2 ± 0.4</td>
</tr>
<tr>
<td>#Metabolisable energy (kJ g⁻¹ OM)</td>
<td>11.5 ± 0.6</td>
<td>10.8 ± 1.0</td>
<td>11.5 ± 0.7</td>
</tr>
<tr>
<td>Nitrogen (% OM)</td>
<td>3.07 ± 0.10</td>
<td>2.96 ± 0.09</td>
<td>3.01 ± 0.10</td>
</tr>
<tr>
<td>Neutral detergent fibre (% OM)</td>
<td>8.5 ± 0.5</td>
<td>15.6 ± 0.5</td>
<td>16.7 ± 2.5</td>
</tr>
<tr>
<td>Acid detergent fibre (% OM)</td>
<td>3.0 ± 0.0</td>
<td>5.9 ± 0.2</td>
<td>6.9 ± 0.1</td>
</tr>
</tbody>
</table>

Note: "Estimated post-hoc based on data presented in Table 1."
Table 2: Mean (± SD) organ, abdominal fat and liver masses from king quail offered low fibre (LF; n = 6), high fibre balanced (HFB; n = 6), and high fibre unbalanced (HFU; n = 6) diets.

<table>
<thead>
<tr>
<th></th>
<th>LF</th>
<th>HFB</th>
<th>HFU</th>
<th>Diet F or H&lt;sup&gt;g&lt;/sup&gt;</th>
<th>Diet P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Entire gut</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Wet (g)</td>
<td>2.54 ± 0.61</td>
<td>2.86 ± 0.41</td>
<td>3.16 ± 0.43</td>
<td>2.36</td>
<td>0.13</td>
</tr>
<tr>
<td>Dry (mg)</td>
<td>691.5 ± 59.0&lt;sup&gt;A&lt;/sup&gt;</td>
<td>781.5 ± 17.1&lt;sup&gt;A,B&lt;/sup&gt;</td>
<td>912.8 ± 43.4&lt;sup&gt;B&lt;/sup&gt;</td>
<td>9.06</td>
<td>0.01</td>
</tr>
<tr>
<td><strong>Crop</strong></td>
<td></td>
<td></td>
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<tr>
<td>Wet (mg)</td>
<td>68.7 ± 15.4</td>
<td>85.5 ± 28.4</td>
<td>103.3 ± 22.1</td>
<td>3.52</td>
<td>0.06</td>
</tr>
<tr>
<td>Dry (mg)</td>
<td>16.7 ± 5.5</td>
<td>20.3 ± 7.5</td>
<td>23.8 ± 7.7</td>
<td>1.60</td>
<td>0.24</td>
</tr>
<tr>
<td><strong>Proventriculus</strong></td>
<td></td>
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<tr>
<td>Wet (mg)</td>
<td>179.0 ± 23.9</td>
<td>202.1 ± 32.0</td>
<td>228.3 ± 50.1</td>
<td>2.66</td>
<td>0.10</td>
</tr>
<tr>
<td>Dry (mg)</td>
<td>43.7 ± 6.6</td>
<td>49.3 ± 7.8</td>
<td>56.8 ± 12.2</td>
<td>3.10</td>
<td>0.08</td>
</tr>
<tr>
<td><strong>Gizzard</strong></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Wet (g)</td>
<td>1.16 ± 0.11&lt;sup&gt;X&lt;/sup&gt;</td>
<td>1.39 ± 0.28&lt;sup&gt;X,Y&lt;/sup&gt;</td>
<td>1.64 ± 0.21&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>7.79</td>
<td>0.005</td>
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<tr>
<td>Dry (mg)</td>
<td>340.2 ± 27.0&lt;sup&gt;A&lt;/sup&gt;</td>
<td>404.2 ± 93.5&lt;sup&gt;A,B&lt;/sup&gt;</td>
<td>473.3 ± 48.2&lt;sup&gt;B&lt;/sup&gt;</td>
<td>6.76</td>
<td>0.008</td>
</tr>
<tr>
<td><strong>Small Intestine</strong></td>
<td></td>
<td></td>
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<tr>
<td>Wet (mg)</td>
<td>808.0 ± 201.9</td>
<td>896.9 ± 231.8</td>
<td>1113.3 ± 244.1</td>
<td>2.88</td>
<td>0.09</td>
</tr>
<tr>
<td>Dry (mg)</td>
<td>235.0 ± 34.2</td>
<td>247.0 ± 67.0</td>
<td>289.8 ± 62.0</td>
<td>1.57</td>
<td>0.24</td>
</tr>
<tr>
<td><strong>Caeca</strong></td>
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<td></td>
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</tr>
<tr>
<td>Wet (mg)</td>
<td>137.8 ± 9.9</td>
<td>143.6 ± 15.3</td>
<td>171.3 ± 36.5</td>
<td>4.99</td>
<td>0.08</td>
</tr>
<tr>
<td>Dry (mg)</td>
<td>39.0 ± 5.5</td>
<td>41.5 ± 17.0</td>
<td>48.3 ± 13.4</td>
<td>0.84</td>
<td>0.45</td>
</tr>
<tr>
<td><strong>Rectum-Cloaca</strong></td>
<td></td>
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</tr>
<tr>
<td>Wet (mg)</td>
<td>77.7 ± 14.3</td>
<td>78.8 ± 23.0</td>
<td>88.4 ± 14.7</td>
<td>0.65</td>
<td>0.54</td>
</tr>
<tr>
<td>Dry (mg)</td>
<td>17.0 ± 4.9</td>
<td>19.2 ± 6.1</td>
<td>20.7 ± 4.2</td>
<td>0.77</td>
<td>0.48</td>
</tr>
<tr>
<td><strong>Liver (wt; g)</strong></td>
<td>1.19 ± 0.16&lt;sup&gt;A,B&lt;/sup&gt;</td>
<td>1.30 ± 0.15&lt;sup&gt;B&lt;/sup&gt;</td>
<td>1.50 ± 0.20&lt;sup&gt;A&lt;/sup&gt;</td>
<td>4.8</td>
<td>0.02</td>
</tr>
<tr>
<td><strong>Abdominal Fat (wt; g)</strong></td>
<td>1.07 ± 0.68</td>
<td>1.04 ± 0.23</td>
<td>0.73 ± 0.23</td>
<td>1.0</td>
<td>0.39</td>
</tr>
</tbody>
</table>

Note: Within a row, means (± SD) bearing different superscripts are significantly different (<sup>A</sup>).<sup>B</sup> P < 0.05; <sup>X,Y</sup> P < 0.001). <sup>g</sup>Kruskal-Wallis H-statistic (see Methods).
Table 3: Mean (± SD) intakes and metabolisability by king quail offered low fibre (LF; n = 6), high fibre balanced (HFB; n = 6), and high fibre unbalanced (HFU; n = 6) diets.

<table>
<thead>
<tr>
<th></th>
<th>LF</th>
<th>HFB</th>
<th>HFU</th>
<th>Diet F</th>
<th>Diet P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Body mass</strong></td>
<td></td>
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</tr>
<tr>
<td>Initial (g)</td>
<td>52.8 ± 4.8</td>
<td>50.9 ± 2.7</td>
<td>50.8 ± 3.8</td>
<td>0.5</td>
<td>0.62</td>
</tr>
<tr>
<td>Change (% initial)</td>
<td>-0.9 ± 5.2</td>
<td>5.4 ± 6.8</td>
<td>2.8 ± 5.0</td>
<td>1.8</td>
<td>0.19</td>
</tr>
<tr>
<td><strong>Dry matter</strong></td>
<td></td>
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</tr>
<tr>
<td>Gross intake (g d⁻¹)</td>
<td>6.56 ± 0.38</td>
<td>6.55 ± 0.61</td>
<td>6.82 ± 1.03</td>
<td>0.27</td>
<td>0.76</td>
</tr>
<tr>
<td>Metabolisability (%)</td>
<td>72.9 ± 4.8^A</td>
<td>61.4 ± 4.7^B</td>
<td>68.7 ± 2.9^A</td>
<td>11.2</td>
<td>0.001</td>
</tr>
<tr>
<td><strong>Organic matter</strong></td>
<td></td>
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<tr>
<td>Gross intake (g d⁻¹)</td>
<td>5.91 ± 0.35</td>
<td>5.75 ± 0.54</td>
<td>6.14 ± 0.92</td>
<td>0.55</td>
<td>0.59</td>
</tr>
<tr>
<td>Metabolisability (%)</td>
<td>76.6 ± 3.9^A</td>
<td>66.9 ± 4.7^B</td>
<td>70.68 ± 2.2^B</td>
<td>10.1</td>
<td>0.002</td>
</tr>
<tr>
<td><strong>Energy</strong></td>
<td></td>
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</tr>
<tr>
<td>Gross intake (kJ d⁻¹)</td>
<td>107.3 ± 6.3</td>
<td>121.2 ± 11.3</td>
<td>117.2 ± 17.6</td>
<td>1.95</td>
<td>0.18</td>
</tr>
<tr>
<td>Metabolisability (%)</td>
<td>74.7 ± 4.3^A</td>
<td>68.4 ± 4.0^B</td>
<td>71.8 ± 2.5^B</td>
<td>4.28</td>
<td>0.034</td>
</tr>
<tr>
<td><strong>Nitrogen</strong></td>
<td></td>
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<tr>
<td>Gross intake (mg d⁻¹)</td>
<td>201.3 ± 11.8</td>
<td>194.2 ± 18.1</td>
<td>205.4 ± 30.9</td>
<td>0.41</td>
<td>0.67</td>
</tr>
<tr>
<td>Metabolisability (%)</td>
<td>37.3 ± 10.1</td>
<td>28.0 ± 12.0</td>
<td>29.0 ± 5.3</td>
<td>1.71</td>
<td>0.21</td>
</tr>
<tr>
<td><strong>Neutral detergent fibre</strong></td>
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<tr>
<td>Gross intake (mg d⁻¹)</td>
<td>557 ± 32^A</td>
<td>902 ± 84^B</td>
<td>1088 ± 164^C</td>
<td>59.9</td>
<td>&lt;1x10⁻⁴</td>
</tr>
<tr>
<td>Metabolisability (%)</td>
<td>24.4 ± 17.4^A</td>
<td>19.0 ± 11.0^A</td>
<td>48.4 ± 11.4^B</td>
<td>7.99</td>
<td>0.004</td>
</tr>
<tr>
<td><strong>Acid detergent fibre</strong></td>
<td></td>
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</tr>
<tr>
<td>Gross intake (mg d⁻¹)</td>
<td>174 ± 10^X</td>
<td>304 ± 14^Y</td>
<td>345 ± 52^Y</td>
<td>66.8</td>
<td>&lt;1x10⁻⁴</td>
</tr>
<tr>
<td>Metabolisability (%)</td>
<td>14.9 ± 21.7^A</td>
<td>9.8 ± 12.7^A</td>
<td>41.8 ± 13.0^B</td>
<td>6.65</td>
<td>0.008</td>
</tr>
</tbody>
</table>

Note: Within a row, means bearing different superscripts are significantly different (X, Y, Z, P < 0.05, X, Y P < 1x10⁻⁴). *Organic matter = dry mass – ash (see methods).