Gastrointestinal adaptation
The ability of the gastrointestinal (GI) system to modulate its structure and function is an important response to shifting nutritional regimes and to certain disease states. Birds may be particularly good models for studying the adaptability of the gut. Many species have relatively simple guts, making them good systems for studying digestive processes in the stomach-small intestine, uncomplicated by fermentation or extended retention in a voluminous hindgut. Birds have less intestinal mass in relation to body mass than mammals, so some GI adjustments might be particularly pronounced in them. Many wild species exhibit large seasonal shifts in diet composition or daily food intake rate.

In mammals, GI modulation, especially of the absorptive step, has been studied systematically. Modulation of absorption at the intestine’s brush border membrane is of two types—specific and nonspecific. For some nutrients (sugar, amino acids, some vitamins and minerals) changes in dietary concentration lead to specific changes in absorption rates for those nutrients, probably due to altered densities of the specific nutrient transporters. Brush border glucose uptake is increased on high carbohydrate diet, for example. Nonspecific modulation occurs when uptake rates for many nutrients change in the same direction, probably due to increased surface area. Brush border glucose, amino acid, mineral and vitamin uptake rates are increased in lactating mammals which have higher food intake; for example. The explanation of the functional significance of both kinds of modulation is that the intestine’s capacity to absorb nutrients is sufficient to meet normal intake loads, with some spare capacity. But if load increased considerably without upward modulation of transport capacity, then the ‘safety margin’ would be eliminated, or perhaps capacity would become insufficient with resultant decreases in extraction efficiency.

In the following paragraphs I consider to what extent this paradigm of intestinal adaptation applies to omnivorous birds. I also review other GI adjustments of birds to altered food composition and food intake levels.

Tests for modulation of absorption to altered food composition
Four species of omnivorous birds have been tested for their ability to increase intestinal mediated glucose absorption when switched to high carbohydrate diet. In contrast to omnivorous mammals and fish which may double glucose absorption rate on high carbohydrate diet, American Robins, Yellow-rumped Warblers, House Sparrows, and Bobwhite Quail exhibited little or no upward modulation of intestinal brush border mediated transport activity in vitro (Fig. 1). In the warblers, D-glucose uptake was altered in the direction opposite that expected. Along with L-leucine uptake (not shown), glucose uptake in warblers increased positively with increased dietary protein content.

Surprisingly, the glucose mediated uptake rates in all the species were relatively low, too low to explain observed rates of sugar absorption in the whole-animal. This implied that nonmediated glucose absorption predominated. Independent verification of that was sought in nectarivorous Rainbow Lorikeets drinking sugar solutions. We used a pharmacokinetic
Fig. 1. Tests for modulation of intestinal mediated D-glucose uptake in four avian species. Only quail exhibited the expected elevation in uptake rate when acclimated (> 7 days) to high carbohydrate diet. In vitro uptakes are at 50 mM, a saturating concentration, except for the warblers where they are for 1 mM.

Technique to measure in vivo absorption of L-glucose, the stereoisomer that does not interact with the Na+/glucose cotransporter. Eighty percent of L-glucose that was ingested was absorbed, confirming that nonmediated absorption can be substantial. These results pose challenging questions to the widely disseminated view that the transport capacity of apical sugar and amino acid transporters are matched to meet metabolic demands with some provision for a safety margin.

Other GI adjustments to altered food composition

Increased absorption rate is just one of several possible adjustments to increased nutrient concentration that would maintain digestive efficiency. Others include increased substrate hydrolysis rates and prolonged retention time.

There have been less than a dozen studies of modulation of digestive enzymes within avian species, almost all with chickens and turkeys. They show the same patterns that are apparent in mammals: levels of the major pancreatic digestive enzymes (proteases, amylase, lipase), and some intestinal brush border enzymes (aminopeptidase N, maltase, sucrase) change in proportion to the dietary content of their respective substrates.

Retention time also appears to be adjusted to diet composition. Generally, in birds gastric emptying is stimulated by intragastric volume and inhibited by negative feedback arising from duodenal and ileal receptors stimulated by products of digestion of food. An analogous negative feedback on transit in the intestine has been termed the ‘ileal brake’. It may be present in birds because the transit times of markers are longer in hens and Yellow-rumped Warblers fed higher fat diets and in American Robins fed insects vs fruits. In Robins the longer transit time was attributed to altered motility patterns because there were no concurrent change in intestinal volume. Evidence is increasing that modulation of digesta flow is an important adaptation of wild omnivorous birds to altered food composition (Table 1).
Table 1. Experimental evidence for modulation of digesta residence time.

<table>
<thead>
<tr>
<th>Bird</th>
<th>Manipulation</th>
<th>Change in residence time</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cedar Waxwing</td>
<td>Switched from 2% to 30% sugar in fruit</td>
<td>50% increase in mouth-to-anus retention time</td>
<td>*</td>
</tr>
<tr>
<td>Rainbow Lorikeet</td>
<td>Switched from 0.4 M to 1.2 M glucose in nectar</td>
<td>100% longer stomach retention time</td>
<td>6</td>
</tr>
<tr>
<td>American Robin</td>
<td>Switched from fruit to insects</td>
<td>150% longer transit time</td>
<td>5</td>
</tr>
<tr>
<td>Yellow-rumped Warbler</td>
<td>Switched from low-fat to high-fat diet</td>
<td>78% increase in mouth-to-anus mean retention time</td>
<td>6</td>
</tr>
</tbody>
</table>

* D.J. Levey (pers. communication).

GI adjustments to higher daily food intake rate
Consideration of digestion models suggests that higher digesta flow rate might be compensated for in a number of ways that would maintain digestive efficiency: (1) if the GI tract enlarges, the exposure time of ingested particles to GI processes (retention time) is unchanged; (2) no change in retention time, but the GI processes (reaction rates) themselves speed up. Effective discrimination of these alternatives requires simultaneous measurement of all the variables. This was achieved in only one study so far, and the results matched the first scenario. In studies with insectivorous House Wrens that were acclimated to cold, daily food intake doubled, gut mass and volume increased 25-35%, mouth-to-anus retention time and amino acid uptake rates per unit small intestine did not change significantly, and there was no decrease in digestive efficiency. Other more fragmentary data on herbivorous and omnivorous birds also indicate that the primary adjustment to increased feeding rate, due either to cold or low quality food, is an increase in GI tract volume (Table 2).

Table 2. Experimental evidence of the morphological plasticity of the avian intestine.

<table>
<thead>
<tr>
<th>Bird</th>
<th>Manipulation</th>
<th>Change in intestine</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Japanese Quail</td>
<td>Acclimation to low temperature</td>
<td>30% increase in length</td>
<td>14</td>
</tr>
<tr>
<td>House Wren</td>
<td>Acclimation to low temperature</td>
<td>35% increase in mass</td>
<td>13</td>
</tr>
<tr>
<td>Japanese Quail</td>
<td>Acclimation to poor diet</td>
<td>10% increase in length</td>
<td>15</td>
</tr>
<tr>
<td>Woodpigeon</td>
<td>Acclimation to poor diet</td>
<td>40% increase in length</td>
<td>16</td>
</tr>
<tr>
<td>Starling</td>
<td>Acclimation to poor diet</td>
<td>20% increase in length</td>
<td>17</td>
</tr>
</tbody>
</table>

In summary, the avian GI tract exhibits considerable flexibility in the face of altered food composition and level of intake. The primary adjustment to increased feeding rate is an enlarged gut. The net effect is to maintain retention time and hence digestive efficiency constant with increased load. Increased tissue specific rates of chemical breakdown and, in some cases absorption, occur when dietary substrate levels increase. However, passive glucose absorption is apparently substantial in some cases, and whether it is modulated remains unknown. Additionally, increased dietary substrate levels tend to increase digesta residence time. The net effect of increased reaction rates, and contact time between digesta and the digestive processes, is to maintain digestive efficiency when load is increased.

Acknowledgements: Supported by NSF BSR-9020280. Thanks to D.J. Levey for sharing unpublished data.


