Compensatory feeding in response to variable food quality by *Melanoplus differentialis*

**YUELONG YANG** and **ANTHONY JOERN**
School of Biological Sciences, University of Nebraska, U.S.A.

**Abstract.** The behavioural mechanisms driving compensatory food consumption in response to dietary dilution as well as the relationship between feeding time and food residence time (i.e. digesta retention time in the gut) were studied using the non-diapausing strain of the grasshopper *Melanoplus differentialis* (Thomas) (Orthoptera: Acrididae). 3-day-old, sixth-instar nymphs and 3-day-old adults were fed artificial diets containing 1%, 3% and 5% total nitrogen (N) at 30°C, LD 14:10 h; the feeding behaviour was recorded using electronic monitoring devices connected to microcomputers for 24 h. The percentage of time spent feeding increased linearly as diets were diluted using non-digestible cellulose from 5% to 1% N. This response was due to an increase in the number of meals while the meal duration of a feeding bout was unaltered. Sixth-instar nymphs spent about 40% more time feeding than the larger adults. The increased feeding time in nymphs resulted from both more frequent feeding bouts and longer meal duration. Feeding time and food residence time were highly negatively related.

**Key words.** Artificial diet, body size, compensation, electronic feeding device, feeding behaviour, food residence time, grasshopper, intermeal duration, meal duration, meal number.

**Introduction**

Detailed analysis of behaviour can be an effective means of providing insights into the mechanisms underlying complex processes such as feeding responses to variable food quality (Simpson, 1982). Much is known about factors affecting meal initiation, duration and termination in the final instar nymphs of the African migratory locust, *Locusta migratoria*, because of the detailed analyses of their feeding patterns (Bernays & Chapman, 1972; Blaney *et al.*, 1973; Simpson, 1982, 1983, 1990; Simpson & Ludlow, 1986; Simpson *et al.*, 1988). However, in order to generalize results obtained from *L. migratoria* it is necessary to investigate feeding patterns of different developmental stages as well as responses by many different insect species (Roessingh & Simpson, 1984; Joern *et al.*, 1986; Reynolds *et al.*, 1986; Timmins *et al.*, 1988; Chapman & Beerling, 1990; Blust & Hopkins, 1990; Timmins & Reynolds, 1992).

Insects utilize compensatory responses to maintain an optimal or near-optimal performance and thus mitigate the impact of a changing environment. Adaptive compensation by insect herbivores in response to altered food quality has been extensively investigated from a variety of viewpoints, especially: dietary selection (Messina, 1982; Waldbauer *et al.*, 1984; Abisgold & Simpson, 1987; Simpson *et al.*, 1990; Waldbauer & Friedman, 1991; Simmonds *et al.*, 1992), food consumption (Bailey & Mukerji, 1976; McGinnis & Kasting, 1967; Barton Brown, 1975; Simpson & Abisgold, 1985; Slansky & Wheeler, 1989; Raubenheimer, 1992), and post-ingestive food utilization (Bailey & Mukerji, 1976; Woodring *et al.*, 1979; Mattson, 1980; Scriber & Slansky, 1981; Karowe & Martin, 1989; Jindra & Schnal, 1989; Simpson & Simpson, 1989; Slansky & Wheeler, 1989; Raubenheimer, 1992; Yang & Joern, 1993a, b). However, the direct relationships among specific compensatory responses have seldom been empirically examined within any insect species, although it is recognized that they are often dependent on one another.

Insects feed in bouts, or meals. By varying either meal duration or interfeed duration, insects can control the total percentage of time spent feeding and can therefore manipulate their food consumption to compensate for...
reduced food quality. A number of studies have shown that variability in meal length is regulated by volumetric feedback, a process mediated by gut stretch receptors (Bernays & Simpson, 1982; Simpson, 1983; Simpson & Simpson, 1989).

The food residence time (FRT) is defined as the length of time that digesta is retained inside a digestive tract, and the digestion rate is defined as the amount of limiting nutrient digested from the food per unit of time. We predict that insect herbivores should shorten their food residence time to maintain an optimal or near-optimal digestion rate in response to reduced food quality and/or increased metabolic rate associated with decreased body size (Yang, 1993). This prediction was empirically evaluated and supported (Yang & Joern, 1993b). If a volumetric regulation mechanism through food intake exists, we hypothesized that grasshoppers would spend more time feeding in response to shortened FRT because of the proposed interdependence between feeding and digestion processes. Here, we use the grasshopper *Melanoplus differentialis* (Thomas) (Orthoptera: Acrididae) to examine: behavioural mechanisms employed to compensate for reduced food quality due to diet dilution and increased metabolic rate presumably associated with smaller body sizes; and the assumption that feeding time and FRT are negatively correlated. In addition, we assessed sex-specific feeding responses.

### Materials and Methods

**Experimental animals.** We used the non-diapausing strain of the generalist-feeding grasshopper species *Melanoplus differentialis* in our experiments (Oma et al., 1990). It is a mixed feeder, eating both grasses and forbs, including agricultural products such as corn, alfalfa and various garden products. Nymphs pass through six instars and adults are relatively large in size. Previous experiments documented that 3-day-old adults weighted twice as much as 3-day-old sixth-instar nymphs (Yang & Joern, 1993a). The fresh body weight of newly moulted male and female adults are 0.61 ± 0.01 g (n = 29) and 0.78 ± 0.02 g (n = 20), respectively; and the fresh body weight of newly moulted male and female sixth-instar nymphs are 0.29 ± 0.01 g (n = 18) and 0.37 ± 0.01 g (n = 17), respectively. We raised grasshoppers at 30°C, LD 14:10h while feeding them barley seedlings until they reached the fourth stadium. At this juncture we supplied grasshoppers dry and wet artificial diets (see below) containing 3% total nitrogen and 3% total non-structural carbohydrate (TNC), along with the barley seedlings, until individuals reached the last nymphal stadium when experiments commenced.

**Artificial diets.** Agar-based artificial diets containing commercially prepared Purina Horse Charge® (Table 1) allowed us to manipulate the food quality quantitatively. Horse Charge is a horse feed supplement containing high-quality protein fortified with vitamins and minerals. Ingredients include: plant protein products, grain products, forage products; processed grain by-products, molasses products, animal fat preserved with ethoxyquin, vitamin A, E, B12 and D3 supplements, riboflavin supplement, calcium pantothenate, calcium carbonate, sodium selenite, dicalcium phosphate, calcium iodate, salt, cobalt carbonate, ferrous carbonate, copper sulphate manganese oxide and zinc oxide. *M. differentialis* survived, developed and reproduced well when fed only Horse Charge, starting from the fourth instar. Chemical analysis of Horse Charge showed that total nitrogen and total non-structural carbohydrate (TNC) each constituted 6% of the total dry weight. We manipulated food quality by diluting Horse Charge with non-digestible cellulose to 1%, 3% and 5% total nitrogen in the diet. All dietary components were diluted simultaneously and TNC levels varied with total N in a 1:1 fashion. For convenience, we refer to N content as a measure of diet quality, but energy, energy plus protein or some combination including trace nutrients may be the key for understanding the specific nutritional basis of our results. Initial water content of these diets was 80% in all cases. Water loss rate of similar-sized pieces of diet through evaporation in the environmental chamber was 6% per hour, on average, and independent of diet quality. Since food was replaced often, water was seldom limiting to individuals in these experiments. Dry artificial diets were composed of only ground Horse Charge. Composition and preparation of wet artificial diets are described in Table 1.

**Feeding monitor.** An inexpensive electronic device, modified from that of Blust & Hopkins (1990), was used to monitor the feeding activity of each test insect (Fig. 1). Blust & Hopkins’s (1990) electronic device worked well when grasshoppers fed on living plants, but was not sufficiently stable on artificial diets. We modified the circuit to solve this problem (Fig. 1).

### Table 1. Composition and preparation of artificial diets containing 80%, water and 1%, 3% and 5% total nitrogen or total nonstructural carbohydrate (TNC).

<table>
<thead>
<tr>
<th>Component</th>
<th>1%</th>
<th>3%</th>
<th>5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agar (g)</td>
<td>5.56</td>
<td>5.56</td>
<td>5.56</td>
</tr>
<tr>
<td>Sorbic acid (g)</td>
<td>0.44</td>
<td>0.44</td>
<td>0.44</td>
</tr>
<tr>
<td>Methylparaben (g)</td>
<td>0.38</td>
<td>0.38</td>
<td>0.38</td>
</tr>
<tr>
<td>Horse Charge® (g)</td>
<td>8.65</td>
<td>25.94</td>
<td>43.23</td>
</tr>
<tr>
<td>Cellulose (g)</td>
<td>36.85</td>
<td>19.56</td>
<td>2.27</td>
</tr>
<tr>
<td>Distilled water (ml)</td>
<td>207.50</td>
<td>207.50</td>
<td>207.50</td>
</tr>
</tbody>
</table>

Preparation procedure: (1) mix agar with boiling water and cool the solution to 65–70°C; (2) add and mix thoroughly the sorbic acid, methylparaben, ground Horse Charge and cellulose; and (3) cool the artificial diets at room temperature for several hours and then store in tightly-covered shoe boxes in the refrigerator. For the diets used for quantifying food residence time, we added 0.26 g (0.5% d.w. of diets) carmine red dye, which was bound to cellulose in diets, to the above components and simultaneously subtracted equal amounts of cellulose. The diets can be stored in tightly-covered plastic shoe-boxes in the refrigerator for 2–3 weeks.
This op-amp circuit is a basic comparator that monitors two input voltages. The voltage through the inverting input \((-\)
 of the op-amp is the reference voltage \(V_{\text{ref}}\), while the voltage through the non-inverting input \(+)\), \(V_{\text{in}}\), indicates a feeding response. When a grasshopper is not feeding, the circuit is open, \(V_{\text{in}} = 0 \text{mV} < V_{\text{ref}}\). When a grasshopper starts feeding, the circuit is closed and \(V_{\text{in}}\) rises above \(V_{\text{ref}}\), so that the op-amp changes its output state from negative voltage to positive voltage, and vice versa when feeding ends. This voltage change is filtered and amplified through the 1N914 diode and the 2N2222 transistor, and can then be detected by the computer. The voltage changes can also be detected by either observing the light-emitting diodes or reading a message on the computer monitor. The time when the op-amp changes its output voltage state is saved into a sequential data file on a floppy diskette. \(V_{\text{ref}}\) can be changed to obtain the voltage needed for detecting biting (compared with mere bodily contact between the diet and grasshopper) on different types of food (e.g. living plant and artificial diet) by varying the resistance of the 10 k\,\Omega potentiometer.

We employed a BASIC program for detecting and recording the time when the circuit output voltage changed in response to the initiation and termination of meals. 4 min was used as the feeding bout criterion, as suggested by Simpson (1982). Twelve electronic circuits were used to record the temporal feeding patterns of twelve grasshoppers simultaneously in order to examine the feeding pattern of two developmental stages (sixth nymphal stadium and adult stage) and both sexes on three diets. Visual observation confirmed that the recording system was very accurate and reliable. Time spent feeding can be underestimated when grasshoppers feed on living plants because the grasshoppers can cut off pieces of leaves before eating them, thus breaking the circuit. This is seldom a problem on artificial diets.

**Experimental design and set-up.** We used a \(3 \times 2 \times 2\) factorial experiment in a completely randomized design to examine the effect of three levels of food quality (1%, 3%, and 5% N), two developmental stages (sixth nymphal stadium and adult stage) and both sexes on the temporal feeding patterns of *M. differentialis*. Statistical analyses were performed using MGLH (Multiple General Linear Hypothesis) procedure in SYSTAT (Wilkinson, 1989). Univariate analysis of variance was used to examine the influence of food quality, developmental stages (body sizes) and sex on feeding time, meal numbers, intermeal duration and meal duration. Fisher's LSD was used for multiple mean comparisons. Results were presented in the format of mean ± standard error.

As soon as a grasshopper moulted to either the sixth stadium or adult stage, we randomly assigned each individual grasshopper to one of the three artificial diets (1%, 3% and 5% N diets). Grasshoppers were individually-caged (8 cm in diameter and 10 cm in height) and fed their assigned diets for 2 days in an environmental chamber at 30°C, LD 14:10 h. The cages were constructed of insulated screen with the top and bottom covered tightly. The temporal feeding pattern of the grasshoppers was recorded for 24 h, beginning with the third day.

Diet was replaced four or five times during the 24 h testing period. The artificial diet was linked to the circuit using wire-wrap wire with a wire-wrapping post soldered at the end to facilitate changing food. We used hair-like...
thin wire taken from small transformers to connect the grasshopper to the circuit. As suggested by Blust & Hipkins (1990), the wire was implanted beneath the pronotum of a grasshopper and held in place by a drop of melted beeswax. Our observations confirmed that the wire had no detectable effect on feeding and movement of the test grasshoppers. In fact, several grasshoppers successfully moulted during the early testing period when a grasshopper was randomly selected from the stock and tested for several days. Each piece of transformer wire could be used several times. If a wire was broken during the 24 h test period, the data associated with that run were discarded.

Food residence time (FRT) is the time that the digesta is retained in the gut of a grasshopper. FRT was quantified using methods described in Yang & Joern (1993b). In brief, we collected the faecal pellets (both dried and undyed) using a modified fraction collector (commonly used by biochemists) where a piece of plastic screen and a funnel attached to the bottom of the test cage ensured that faecal pellets fell into the test tubes moving along a track at 3 min intervals. We estimated the length of time that each faecal pellet spent in the gut beginning from the end of the dried treatment meal. FRT was expressed as the median instead of the mean of the time when the red pellets were excreted because the median was less affected by extreme values.

To examine the general relationship between the percentage of time spent feeding and food residence time (FRT) within the gut, we performed a regression analysis on the average feeding time in relation to the average food residence time. As we previously noted (Yang & Joern, 1993b), FRT could not be directly and independently manipulated in *M. differentialis*. The effect of FRT was investigated indirectly by manipulating food quality as well as by comparing different developmental stages. Previous studies (Yang & Joern, 1993b) have demonstrated that *M. differentialis* increased FRT to compensate for reduced food quality or increased metabolic rate, presumably because of smaller body size. Here, we examined the feeding responses to the same treatments as in previous studies. In order to have a large enough range of FRT and total feeding time to evaluate their relationship, we grouped the experimental grasshoppers based on their developmental stage, sex and the quality of diet fed. We estimated the mean FRT and the mean feeding time for each group and then performed a regression analysis. The analysis is unavoidably confounded by food quality, developmental stage and sex, but it provides appropriate insights regarding the interdependence between feeding and digestive responses.

### Results

#### Feeding time

The percentage time spent feeding was greatly affected by diet quality, body size and their interactions (Table 2). Feeding time decreased linearly with increased diet quality in both 3-day-old adults (1% N: 13.82 ± 1.11, n = 20; 3% N: 9.13 ± 0.45, n = 22; 5% N: 6.28 ± 0.29, n = 23) and the 3-day-old sixth-instar nymphs (1% N: 20.05 ± 1.08, n = 18; 3% N: 12.61 ± 0.60, n = 21; 5% N: 8.34 ± 0.32, n = 22). Smaller nymphs spent more time feeding at each level of food quality than adults (Fig. 2). The significant diet quality-by body size interaction resulted from the greater difference between the nymphs and adults fed on 1% N diets (Fig. 2).

##### Meal numbers and intermeal duration

Meal numbers were greatly affected by diet quality, sex and body size, without significant interactions (Table 2). Meal numbers decreased as diet quality increased. On average, the number of meals that a grasshopper took within 24 h was 20.82 ± 1.10 (n = 38) on 1% N, 13.49 ± 0.66 (n = 43) on 3% N, and 9.46 ± 0.47 (n = 45) on 5% N diets. Smaller nymphs (15.13 ± 0.91, n = 61) ate more frequently than larger adults (13.57 ± 0.76, n = 65). Males (15.23 ± 0.98, n = 53), on average, ate more frequently than females (13.67 ± 0.73, n = 73).

The intermeal duration was only significantly influenced by diet quality (Table 2). As the diet was diluted from 5% of

### Table 2. Results of univariate analysis of variance of the influence of diet quality (N), body size (B) and sex (S) on the total feeding time (%), meal numbers, intermeal duration, and meal duration in *Melanoplus differentialis*.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Feeding time</th>
<th></th>
<th></th>
<th>Meal numbers</th>
<th></th>
<th></th>
<th>Intermeal duration</th>
<th></th>
<th>Meal duration</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrogen (N)</td>
<td>2</td>
<td>95.855</td>
<td>0.000</td>
<td>61.708</td>
<td>0.000</td>
<td>30.546</td>
<td>0.000</td>
<td>0.439</td>
<td>0.645</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N-linear</td>
<td>1</td>
<td>190.416</td>
<td>0.000</td>
<td>121.127</td>
<td>0.001</td>
<td>60.413</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>N-LOF</td>
<td>1</td>
<td>3.690</td>
<td>0.057</td>
<td>4.566</td>
<td>0.035</td>
<td>0.144</td>
<td>0.705</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sex (S)</td>
<td>1</td>
<td>0.445</td>
<td>0.506</td>
<td>4.562</td>
<td>0.035</td>
<td>2.210</td>
<td>0.140</td>
<td>1.570</td>
<td>0.213</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body size (B)</td>
<td>1</td>
<td>48.635</td>
<td>0.000</td>
<td>6.887</td>
<td>0.010</td>
<td>3.120</td>
<td>0.080</td>
<td>9.309</td>
<td>0.003</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N × S</td>
<td>2</td>
<td>0.155</td>
<td>0.856</td>
<td>0.196</td>
<td>0.823</td>
<td>0.308</td>
<td>0.736</td>
<td>0.038</td>
<td>0.962</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N × B</td>
<td>2</td>
<td>5.252</td>
<td>0.007</td>
<td>2.574</td>
<td>0.081</td>
<td>1.149</td>
<td>0.321</td>
<td>2.200</td>
<td>0.116</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S × B</td>
<td>1</td>
<td>0.315</td>
<td>0.576</td>
<td>2.134</td>
<td>0.147</td>
<td>0.037</td>
<td>0.847</td>
<td>0.044</td>
<td>0.834</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N × S × B</td>
<td>2</td>
<td>1.247</td>
<td>0.291</td>
<td>2.052</td>
<td>0.133</td>
<td>0.228</td>
<td>0.797</td>
<td>2.192</td>
<td>0.116</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>114</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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to 3% and to 1% N, the intermeal duration decreased linearly from 165.81 ± 9.04 min (n = 45) on 5% N diets, to 117.62 ± 6.06 min (n = 43) on 3% N diets, and to 78.78 ± 6.7 min (n = 38) on 1% N diets. On average, nymphs (116.88 ± 7.62 min n = 61) exhibited a shorter intermeal duration than adults (129.56 ± 7.41 min, n = 65) (P = 0.04, one-tailed test). No significant differences in intermeal duration existed between sexes (P = 0.14) (Table 2).

Meal duration

Meal duration was significantly influenced by body size (P = 0.003) (Table 2). Nymphs (13.45 ± 0.58 min, n = 61) spent, on average, 23.3% more time than adults (10.91 ± 0.48 min, n = 65) on each meal. Neither diet quality nor sex had statistically significant effects on meal duration (P = 0.645 and P = 0.213, respectively).

Relationship between feeding time and food residence time

The average percentage of time spent feeding was negatively related to the average food residence time (Fig. 3).

Discussion

The present study is one of a series of studies designed to investigate adaptive compensation in response to changes in food quality in the grasshopper Melanoplus differentialis (Thomas) (Yang & Joern, 1993a, b). In previous studies we demonstrated that M. differentialis compensated for reduced food quality by: (a) increasing digestive capacity through increasing relative gut sizes (Yang & Joern, 1993a), and (b) processing more food per unit of time by decreasing food residence time in the gut (Yang & Joern, 1993b). As a result of compensation, M. differentialis survived equally well and developed equally fast on 3% N diets compared with individuals fed on 5% N diets. However, compensation could not offset further dilution of dietary energy nutrients concentrations, and grasshoppers on 1% N diets exhibited significantly lower survival rates, slower development and reduced weight gain.

In this paper we have demonstrated that M. differentialis also compensated behaviourally for diet dilution. Three major conclusions can be drawn. M. differentialis increased the percentage of time they spent feeding to compensate for both diluted dietary components (such as energy or nutrients) and increased metabolic rate resulting from smaller body sizes. Significant food quality by body size interactions resulted in much longer feeding time in nymphs. When food quality was reduced, increased feeding time resulted from feeding more frequently with the same meal length. Compared to adults, increased feeding time in nymphs resulted both from more frequent feeding and longer meals. Feeding time and food residence time were strongly negatively related.

Dietary dilution and compensatory feeding responses

Feeding compensation in response to dietary dilution has been studied using two approaches: measuring the total amount of diet consumed, and analysing feeding behaviour of the experimental animals conditioned on food varying in quality. Numerous studies have shown that insects generally increased food consumption, thereby processing more food in response to dietary dilution.
(e.g. Dadd, 1960; McGinnis & Kasting, 1967; Simpson & Abisgold, 1985; Slansky & Wheeler, 1989, 1991; Wheeler & Slansky, 1991). Increased food consumption can be achieved by: decreasing intermeal time and thus feeding more frequently as in *Locusta migratoria* (Blaney et al., 1973; Simpson & Abisgold, 1985; Raubenheimer & Simpson, 1990) and in *Schistocerca americana* (Chapman & Berrill, 1990); increasing the meal duration as in *L. migratoria* (Simpson, 1982); and more frequent feeding with longer meals as in *Manduca sexta* (Timmins et al., 1988).

For either *M. differentialis* adults or sixth-instar nymphs, individuals ate more frequently as diet was diluted with non-digestible cellulose while no significant differences existed regarding meal duration. This result differs from that of Timmins *et al.* (1988) who studied the feeding pattern of the fifth-instar larvae of the tobacco hornworm, *Manduca sexta*, in response to dilution of all dietary nutrients. The average meal duration of *M. differentialis* sixth-instar nymphs (13.45 ± 0.58 min, *n* = 61) is much longer than that of *M. sexta* fifth-instar larvae (less than 5 min). However, *M. sexta* (averaging more than fifty meals in 24 h) fed much more frequently than *M. differentialis* nymphs (averaging fifteen total meals in 24 h). Such feeding pattern differences between caterpillars and grasshopper nymphs may be attributed to gut structure differences. The crop in grasshoppers functions as a storage organ in which food can be partially digested whereas the crop in lepidopterans is greatly reduced (Chapman, 1982). However, differences in feeding patterns between grasshopper nymphs and lepidopteran larvae may also result from physiological mechanisms not yet investigated.

In addition, Timmins *et al.* (1988) observed that the average meal duration of *M. sexta* increased with diet dilution. They suggested that this could be due to the necessity of more gut stretching to end a meal of lower quality diet whose energy and nutrient concentrations were low. We propose a possible alternative explanation. Variation in meal duration of *M. sexta* nymphs, fed on different quality food, could result from the gut volume differences between these insects. We have shown that poor quality food can induce significant changes in gut size in *M. differentialis* in 1–2 weeks (Yang & Joern, 1993a). Similar responses may also exist in *M. sexta*.

**Feeding pattern differences between nymphs and adults**

Many studies on feeding patterns have focused on nymphs because feeding behaviour in nymphs is not complicated by such factors as flight, mating, reproduction or senescence, and is thus much easier to interpret than in adults. We found significant differences in feeding patterns between 3-day-old sixth-instar *M. differentialis* nymphs and adults. Sixth-instar nymphs weighed half much as adults (Yang & Joern, 1993a) yet spent almost 40% more time feeding, presumably to compensate for increased metabolic rate. Increased feeding time in nymphs was achieved by more frequent feeding and longer meals.

As a result, the amount of food processed per unit time and per unit body weight was much larger in nymphs than in adults. Different food processing rates could explain the significantly higher weight gain per unit body weight in nymphs than in adults (Yang & Joern, 1993b).

**Feeding and digestion**

We proposed that an individual animal should reduce food residence time to maintain an optimal or near-optimal digestion rate in response to reduced food quality (Yang, 1993). This prediction was supported by our empirical evaluation of the model (Yang & Joern, 1993b). Since feeding and digestion are two consecutive stages of a single process that determines the rate of gain of both energy and nutrients extracted from food, higher rate of food passage should also lead to more frequent feeding and higher percentage of time spent feeding. The strong negative linear relationship between mean feeding time and mean food residence time of *M. differentialis*, observed in this study, is consistent with this prediction. But this differs from that of the fifth-instar nymphs of *Locusta migratoria*. Locusts were able to compensate for a 50% dilution of their dietary protein by reducing intermeal intervals without varying FRT (Abisgold & Simpson, 1987). This was probably because the amount of food eaten in an average meal was voided from the gut within the average intermeal intervals (Simpson & Simpson, 1989). Thus, the interaction between feeding and digestion processes can be very complex. We must ultimately quantify the costs involved in each process so that we can begin to comprehend such complicated relationships and understand how foraging and digestion interact to shape the optimal strategy to maximize the extraction rate of dietary energy and nutrients.

In summary, multiple solutions exist for maintaining an optimal digestion rate to satisfy the energetic and nutritional needs of insects in the face of variable food quality. These solutions interact as a dynamic system. For example, food selection can greatly influence feeding pattern and digestion processes. But food selection is also constrained by the animal's feeding and digestive capabilities as well as by environmental factors such as food availability or the presence of natural enemies. Significant advances regarding insect nutritional compensation within the context of insect—plant relationships have been made from many studies of adaptive food selection, consumption and post-ingestive food utilization. However, to understand fully the underlying mechanisms of nutritional compensation in the context of whole-organism physiology, we need to integrate such adaptive compensatory mechanisms within a dynamic framework (Mangel & Clark, 1988).

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