

Effects of diet quality on performance and nutrient regulation in an omnivorous katydid

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Abstract. 1. Omnivores by definition eat both plants and animals. However, little is known about how diet macronutrient content affects omnivore performance, or the extent to which they can regulate macronutrient intake. We assessed these questions using the salt marsh katydid, *Conocephalus spartinae* Fox (Tettigoniidae).

2. In our first experiment we used artificial diets with different protein–carbohydrate ratios to assess the effects of diet quality on survival, growth, and lipid accumulation. We found that diets with a high protein–carbohydrate ratio negatively affected *Conocephalus* survival. Among surviving individuals growth was not significantly different across the treatments, but lipid content decreased significantly as the protein–carbohydrate ratio of diets increased.

3. In a second experiment we explored the ability of *Conocephalus* to regulate their protein–carbohydrate intake. Results revealed that *Conocephalus* did not feed randomly when presented with two nutritionally complementary foods. A detailed analysis of their protein–carbohydrate intake revealed selection for a protein-biased diet, but a lack of tight regulate of protein–carbohydrate intake.

4. We discuss how key macronutrients can limit omnivores, and how nutritional flexibility may enable omnivores to persist in nutritionally heterogeneous environments.

Key words. digestible carbohydrates, feeding behaviour, foraging, geometric framework, nutrient regulation, nutrition, omnivore, protein, Tettigoniidae.

Introduction

True omnivores (*sensu* Coll & Guershon, 2002) consume both plants and animals, and in terrestrial systems they can influence species and functional diversity (Agrawal & Klein, 2000; Eubanks & Denno, 2000b; Zhi *et al.*, 2006; Ho & Pennings, 2008). As is the case for strict herbivores and predators, food resource limitations can potentially have large impacts on an omnivore's fitness (Kaspari *et al.*, 2001; Jacot *et al.*, 2009; Sasakawa, 2009). However, the ability of omnivores to consume both plant and animal material provides flexibility in adjusting to variable resource supplies. This flexibility could result in a decreased sensitivity to limitations in food resources. A key issue, therefore, is how long can an omnivore tolerate feeding exclusively on plant material in the absence of prey, or alternatively, feeding only on prey.

From an omnivore's perspective, plants and prey are very different in terms of their nutritional profiles, whether considered in terms of elements (e.g. C, N, P, Sterner & Elser, 2002) or macronutrients (protein, carbohydrates, and lipids, Raubenheimer *et al.*, 2009). For example, N and protein, essential building blocks for structural growth and reproduction, are typically found in greater quantities in animal tissue (Matsumura *et al.*, 2004; Taiz & Zeiger, 2006). In contrast, digestible carbohydrates and lipids are functionally similar (i.e. they provide energy). However, lipids have greater caloric value (9 vs. 4 kcal g⁻¹, respectively), thus lipids are 2.25 times more energy-rich than are digestible carbohydrates. Animal tissue typically has greater fat content than plants, but plants tend to have greater amounts of simple and complex digestible carbohydrates (e.g. sucrose and starch, respectively) compared with animal prey items (which contain some simple sugars (e.g. trehalose and glycogen)). All organisms, however, require multiple nutrients simultaneously, so it is most useful to consider the nutrient balance of foods and the extent to

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which the blend of nutrients in a food best meets a given organisms nutritional requirements (Raubenheimer & Simpson, 1999; Behmer, 2009). When plants and prey items are viewed in terms of their position in nutrient space (*sensu* the Geometric Framework; Simpson & Raubenheimer, 1999), plants range from being energy-biased (rich in digestible carbohydrates relative to protein) to having a balanced protein–energy ratios. In contrast, animal prey items tend to have protein–energy ratio that range from equal to protein-biased (R.E.G. Pearson and R.F. Denno, unpublished; Chapman, 1998; Raubenheimer *et al.*, 2009).

When food resources are not limiting, omnivores can mix their diet to more closely match their nutritional needs. Numerous studies have shown that insect herbivores (reviewed by Behmer, 2009), and more recently arthropod predators (Mayntz *et al.*, 2005), actively regulate their nutrient intake, using both behavioural and physiological mechanisms, to redress nutritional imbalances. In the case of both insect herbivores and arthropod predators, nutrient regulation directly optimises performance and fitness (e.g. Mayntz & Toft, 2001; Simpson *et al.*, 2004; Behmer & Joern, 2008; Toft *et al.*, 2010). However, apart from a single study on an extreme generalist cockroach, *Blattella germanica* L. (Blattellidae) (Raubenheimer & Jones, 2006), we know very little about the extent to which omnivores regulate their macronutrient intake, or how the macronutrient composition of available foods influence the fitness of insect omnivores. For example, are omnivores limited more by protein or energy, or do they require a balanced ratio of protein and energy? The nutritional landscape that an omnivore occupies is much broader than that of a strict herbivore or an arthropod predator (Raubenheimer *et al.*, 2009). Therefore, when resources are in abundant supply, omnivores will have ample opportunity to optimise their macronutrient intake by mixing among the available food items.

Omnivory is widespread in nature (Coll & Guershon, 2002; Thompson *et al.*, 2007), so understanding the factors that underlie feeding choices in omnivores is fundamental to the study of population ecology and food-web dynamics (Menge & Sutherland, 1987; Fagan, 1997; Polis *et al.*, 1997; McCann *et al.*, 1998; Rosenheim, 1998; Eubanks & Denno, 2000a,b), as well as to biological control (Rosenheim *et al.*, 1993; Hodge, 1999). Omnivores have either stabilise or destabilise food web dynamics, depending on the relative strength of their effects on plants and prey (Fagan, 1997; Eubanks & Denno, 2000a,b). Understanding the relative importance and potential interactive effects of the various resources that influence omnivore performance helps to elucidate their effects on food web stability. In this study, we hypothesise that the omnivorous salt marsh katydid *Conocephalus spartinae* Fox (Tettigoniidae, hereafter *Conocephalus*) can tolerate a wide range of nutritional ratios, but performs best on diets that have protein–energy content that is protein-biased. Additionally, we predict that *Conocephalus*, when allowed to self-select its diet from among nutritionally complementary foods, actively regulates its protein–energy intake to levels that result in optimal performance.

Methods

Study system

Early instar nymphs of the omnivorous katydid *Conocephalus* were collected during June 2007 at a study site (a mid-Atlantic coast intertidal marsh) located on the Eastern shore of Maryland on Chincoteague Bay (38.13°N, 75.30°W). *Conocephalus* is the most common omnivore at this site, and is recorded as feeding at three different trophic levels (plant leaves and seeds, herbivores, and predators (Vince *et al.*, 1981; Bertness & Shumway, 1992; Gwynne, 2001). The dominant plants, insect herbivores, and invertebrate predators upon which *Conocephalus* is likely to feed, and the average macronutrient content of these respective food items, where available, are described below.

The salt marsh cordgrass *Spartina alterniflora* Loisel (Poaceae, hereafter *Spartina*) is the dominant plant in this system, and *Conocephalus* regularly feeds upon it (Denno, 1983; Gallagher *et al.*, 1988). The N content of *Spartina* can vary, but at this site it typically ranges between 1% and 2% (Matsumura *et al.*, 2004); using a standard conversion factor of 6.25%, this translates into protein content of between ~6 and 13%. With respect to carbohydrates and lipids, McIntire and Dunstan (1976), using *Spartina* plants from Georgia, reported that total non-structural (TNS) carbohydrates [free sugars, disaccharides (sucrose), and storage products such as starch, fructose and other oligosaccharides] ranged from 4 to 10%. Squiers and Good (1974) reported *Spartina* lipid values of about 2% dry mass. The protein–energy nutrient space that *Spartina* typically occupies is shown in Fig. 1; here energy is the summed product of carbohydrates and lipids, but expressed

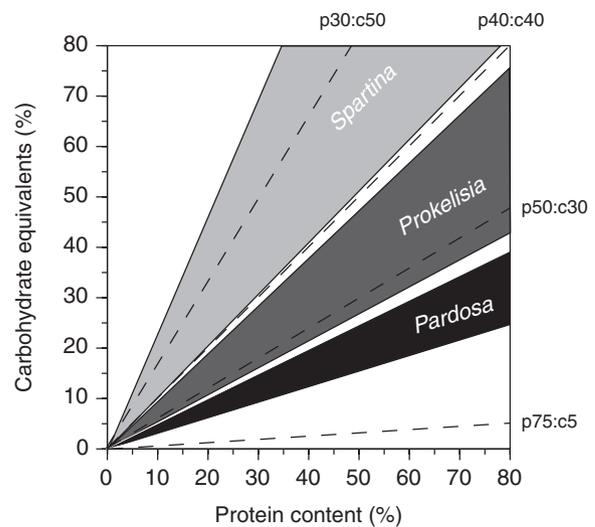


Fig. 1. The protein and energy (carbohydrate equivalent) nutrient space of the foods available to *Conocephalus*. This figure shows marsh representative food items from three trophic levels: a plant (*Spartina*), a herbivore (*Prokelisia*) and a predator (*Pardosa*); see the methods for an explanation of carbohydrate equivalents. The dashed lines show the protein-carbohydrate (p:c) ratios of the four experimental foods used in this study (see the methods for diet making details).

as carbohydrate equivalents, e.g. one lipid unit is equal to 2.25 carbohydrate units (as explained in the Introduction), so the lower energy range of *Spartina* is about 8.5% carbohydrate equivalents [4% from digestible carbohydrates, plus 4.5% from lipids (2% lipid \times 2.25 carbohydrate equivalents); the higher range is about 14.5% carbohydrate equivalents]. It is also worth noting that *Spartina* contains plant secondary compounds (particularly phenolics). In its southern range phenolics can occur at concentrations that deter herbivores (Pennings *et al.*, 1998; Salgado & Pennings, 2005); at *Spartina*'s northern range (our study site) phenolics occur at lower concentrations and do not deter orthopteran herbivores (Siska *et al.*, 2002; Salgado & Pennings, 2005).

Hemipteran sap-feeders (planthoppers, leafhoppers, and mirid bugs) are the most abundant insect herbivores at our study site (Denno *et al.*, 1980; Denno, 1983; Denno & Peterson, 2000), with two phloem-feeding planthoppers, *Prokelisia dolus* and *P. marginata* (Delphacidae), the most plentiful (Denno *et al.*, 2000). The dry N content of these two planthoppers has been measured at approximately 9%, or about ~56% protein (Matsumura *et al.*, 2004). In contrast to plants, invertebrates (including planthoppers) generally have lower levels of TNS carbohydrates, and higher levels of lipids. In the case of hemipterans at our site, typical TNS carbohydrate levels would be 1–2% (a combination of trehalose glycogen; Becker *et al.*, 1996), while lipid levels range between 17% and 21% (Pearson, 2009). When lipids are converted to carbohydrate equivalents, the protein–energy content of planthoppers ranges from equal-ratio to protein-biased (Fig. 1).

Finally, the most abundant invertebrate predators at this site are wolf spiders, particularly *Pardosa littoralis* (Lycosidae; Dobel *et al.*, 1990; Denno *et al.*, 2002). Their dry N content is estimated at about 12% (Matsumura *et al.*, 2004), giving them a protein content of ~75%. Their TNS carbohydrate levels are likely similar to planthoppers, and their lipid levels range from 12% to 18% (Salomon *et al.*, 2008; Jensen *et al.*, 2010); the likely protein–energy values that *Pardosa* spiders provide is shown in Fig. 1.

Performance on different diets

In our first experiment we explored how food protein and energy content affected *Conocephalus* survival and growth. We did this by creating experimental foods that differed in their protein and digestible carbohydrate content [as outlined in Dadd (1961), and modified by Simpson and Abisgold (1985)]. Although *Conocephalus* food contains energy in the form of both digestible carbohydrates and lipids, for simplicity we provided energy only in the form of digestible carbohydrates (henceforth simply carbohydrates). In total, four diets were generated: (i) p30 : c50 (30% protein and 50% carbohydrate), (ii) p40 : c40, (iii) p50 : c30, and (iv) p75 : c5. These diets (with the exception of the heavily biased protein diet) fall across the protein–energy nutritional space that *Conocephalus* would encounter under natural conditions in the field (Table S1; Fig. 1). It is worth noting that all the foods contain identical macronutrient content (80%); this was done to prevent confounding factors associated with nutrient dilution (an

interesting topic, but not addressed in the current study). The remaining 20% of each diet had identical proportions of other ingredients, including vitamins, cholesterol, salts, fatty acids and cellulose (Table S1). We presented the food suspended in a 1% agar solution, at a 1 : 6 dry diet to agar ratio (Lee *et al.*, 2004). Treatments were replicated 10 times (five individual males and five individual females).

We collected early instar *Conocephalus* using a sweep net and kept them for 48 h with only a water source prior to the experiment. Immediately prior to the start of the experiment, the starting wet-weight mass of each *Conocephalus* was measured and individuals were assigned randomly to circular feeding arenas (15 cm diameter; 6 cm height) that housed four evenly spaced feeding dishes each containing the same diet and a water source in the centre. All of the cages were maintained in a growth chamber at a temperature of 27 °C under a LD 13 : 11 h cycle to approximate summer conditions. We separated the cages with partitions so that *Conocephalus* could not see each other. The experiment was conducted over the course of 12 days. Every 2 days we monitored the units for *Conocephalus* survival and replaced food and water sources.

Following the completion of the experiment we weighed the surviving *Conocephalus* and stored them in a –20 °C freezer for further processing. Lipid content of individuals was determined by first drying individuals in a 60 °C oven and weighing them to the nearest 0.001 mg. We extracted lipids from the dried *Conocephalus* using a chloroform wash (Loveridge, 1973). Here *Conocephalus* were suspended three times in succession in a chloroform bath for 24 h. Following this procedure they were dried at 60 °C in a drying oven to a constant mass and then reweighed. Lipid mass was calculated as the difference in the two mass measurements.

Analyses for the performance measures of survival and growth proceeded first by ANOVA confirming that the initial mass of insects did not differ significantly across treatments (SAS: Proc Mixed). Likewise, there was no effect of gender on any of the performance variables tested; gender as an effect was therefore removed from all future analyses. Next we analysed *Conocephalus* survival on the different treatments using the non-parametric log-rank test (SAS: Proc Lifetest). Data were right-censored to account for the individuals that did not die by the time the experiment ended. To determine if *Conocephalus* survival was related to initial mass we performed a *post hoc* test using ANOVA with mass as the response and survival as a factor with two levels (SAS: Proc Mixed).

All of the analyses for growth used *Conocephalus* individuals that survived the duration of the experiment. The best fitting models for mass gained and lipid mass were selected with Akaike Information Criterion, which accounts for variance explained and the number of parameters. To examine the effect of diet composition on *Conocephalus* growth we analysed total mass gained using ANCOVA (SAS: Proc GLM) with diet type as the explanatory variable and initial mass as a covariate. We analysed the data for differences in lipid mass of the *Conocephalus* on the different diets using ANOVA (SAS: Proc Mixed) with multiple comparisons using diet type and initial mass as the explanatory variables.

Food and nutrient regulation

To determine whether omnivorous early instar *Conocephalus* nymphs regulate their feeding behaviour, we performed a choice experiment in which individuals were presented with pairs of nutritionally complementary foods. The four diets were the same as those used in the first experiment above ('Performance on different diets'), except that we assigned three treatments: (i) p30 : c50 paired with p75 : c5, (ii) p40 : c40 paired with p75 : c5, and (iii) p50 : c30 paired with p75 : c5. Each treatment had 10 replicates (5 males and 5 females) for a total of 30 experimental units. *Conocephalus* were collected in the field in June 2007 and maintained before and during the experiment in the same manner as above. These experiments were completed over a 6-day period, and the diet cubes in each arena were replaced every 48 h with a fresh cube. Cubes were weighed both before placement in the arena and at the end of the 48 h feeding period. To determine the amount of each diet consumed, we first assumed that there was minimal loss of water during the time that the food was in the cage because of how the cage was constructed (minimal venting) and the condition of the food when it was removed. Therefore, from the initial weight of the cube, the final weight and the amount of water (75%) in the diet were subtracted. These data were analysed using *t*-tests to compare the difference in the mean amount of diet consumed in each treatment for three time periods (days 0–2, 2–4, and 4–6), and over the entire experiment (days 0–6).

Two approaches were employed to determine if the *Conocephalus* regulated their dietary intake of proteins and carbohydrates. First, we scored whether the insects fed randomly. Here a two-tailed, one sample *t*-test was used to compare the amounts of the two different foods eaten. Next, we used a MANOVA approach to compare the protein–carbohydrate intake points for each treatment, with gender and initial mass as additional explanatory variables (SAS 9.1.2). Again, the amount of water in each of the diets (75%) was subtracted before analysis was completed. These data were analysed for three time periods (days 0–2, 0–4, and 0–6). For each of the three time periods, the protein and carbohydrate consumed met the assumptions of homogeneity of variance and normality required to perform ANOVA.

Results

Performance on different diets

The log-rank test indicated that survival was poorest on the highly protein-biased diets (p75 : c5; Fig. 2) and there was an overall difference in survival between the treatments over the 12 days of this experiment ($\chi^2 = 12.80$, $P = 0.005$). There was a slight decrease in survival on the p50 : c30 diet, but this difference was not significant compared with survival on the p40 : c40 and p30 : c50 diets. Initial mass at the start of the experiment did not affect survival ($F_{1,37} = 1.23$, $P = 0.274$).

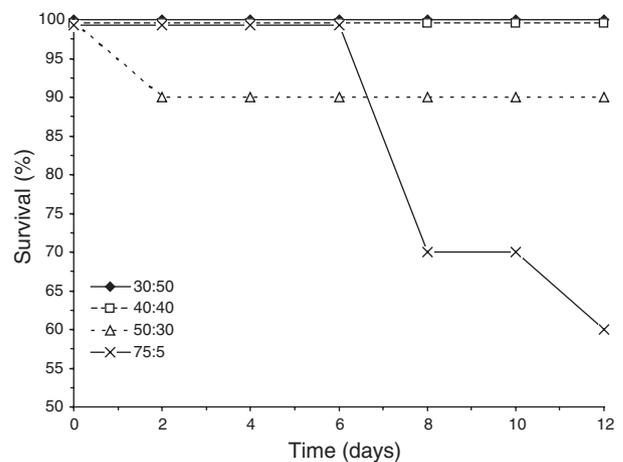


Fig. 2. Percent survival for each of the diet treatments. Pairwise comparisons showed a significant difference in the percent survival of *Conocephalus* in the 75:5 treatment group compared to 30:50 group ($p = 0.0417$), the 40:40 group ($p = 0.0315$) and the 50:30 group ($p = 0.0315$).

There was a main effect of initial mass on mass gained ($F_{1,24} = 10.07$, $P = 0.004$; Fig. 3a), but there was no significant treatment effect ($F_{3,24} = 1.54$, $P = 0.231$), or treatment-by-initial mass interaction ($F_{3,24} = 1.27$, $P = 0.306$). Analysis of lipids in the *Conocephalus* carcasses showed a significant treatment effect ($F_{3,31} = 14.56$, $P < 0.0001$; Fig. 3b) and a significant effect of initial *Conocephalus* mass ($F_{1,31} = 22.72$, $P < 0.0001$). In general, lipid body content decreased as the protein–carbohydrate ratio of the food decreased. Lipid contents were highest on the p30 : c50 (17.51% \pm 1.47) and p40 : c40 (15.06% \pm 0.87) diets, intermediate on the p50 : c30 diet (12.56% \pm 0.96), and lowest on the p75 : c5 diet (6.64% \pm 0.97; Fig. 3b).

Food and nutrient regulation

When the diets differed significantly in their composition (p30 : c50 paired with p75 : c5; p40 : c40 paired with p75 : c5), *Conocephalus* preferred the protein-biased diet, but when the diet compositions were less divergent (p50 : c30 paired with p75 : c5), they ate similar amounts of both (Fig. 4). On the treatment containing p30 : c50 food *Conocephalus* showed a significant preference for the highly protein-biased food (p75 : c5) during two time periods (0–2 days and 2–4 days), and summed over the entire time period. Individuals on the treatment containing p40 : c40 food showed a significant preference for the p75 : c5 food during two of the time periods, and when summed over the entire time period. In contrast, when p50 : c30 and p75 : c5 food was paired, no significant preference was detected.

Having shown that feeding was not a random process, we next used MANOVA approaches to test whether *Conocephalus* tightly regulated their protein–carbohydrate intake; if the intake points for each diet pairing overlapped, we would conclude that *Conocephalus* is capable of tight nutrient

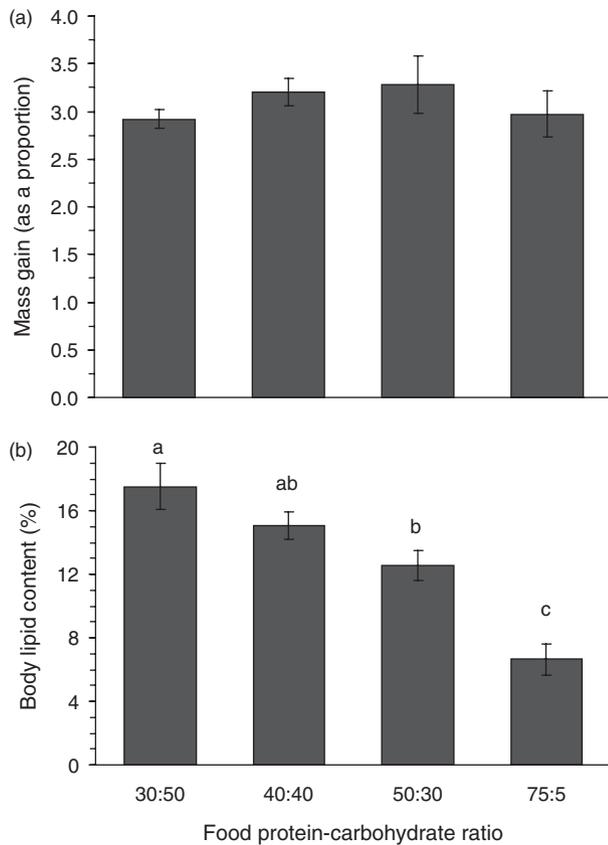


Fig. 3. A) *Conocephalus* mean proportion mass gain (\pm SE) in the four diet treatments. Mean proportion gain was calculated as the final *Conocephalus* mass/initial *Conocephalus* mass; B) Comparison of the mean percent body lipids (\pm SE) of the *Conocephalus* carcasses fed one of four diets differing in protein carbohydrate (P:C) diet treatment for twelve days. Means with different letters are significantly different ($P < 0.05$).

regulation (e.g. Raubenheimer & Jones, 2006). We observed a significant treatment effect for each of the 2-day periods (Day 2: $F_{4,54} = 10.03$, $P < 0.0001$; Day 4: $F_{4,54} = 11.59$, $P < 0.0001$; Day 6: $F_{4,54} = 13.24$, $P < 0.0001$; Fig. 5). Paired contrasts were then used to explore this outcome in greater detail, and here we found significant differences in the total amount of protein and carbohydrate eaten for each of the three pairs (p30 : c50 vs. p40 : c40, p30 : c50 vs. p50 : c30 and p40 : c40 vs. p50 : c30), and at each of the three time periods. Gender did not significantly affect protein–carbohydrate intake, nor was there an effect of initial mass or an interactive effect between treatment and initial mass.

Discussion

Omnivores are important players in terrestrial food webs (e.g. Fagan, 1997; Eubanks & Denno, 2000b) but currently we know very little about what constitutes an optimal diet for them. Denno and Fagan (2003) suggested that omnivores in terrestrial systems are likely to be protein limited, but our findings accord

more closely with a recent paper by Raubenheimer *et al.* (2009) that suggests predators may in fact be energy limited, because their diets are more likely to be deficient in carbohydrates or lipids. Recent empirical work by Hawlena and Schmitz (2010) suggests that energy limitation may depend on the context: the stress of predation risk increased carbohydrate metabolism in orthopteran herbivores. In the field, under natural conditions, *Conocephalus* consumes a mixed diet of plants (leaves, pollen, and seeds; Bertness & Shumway, 1992; Sala *et al.*, 2008) and animal prey [confirmed by Vince *et al.* (1981) who found insect remains in their frass]. However, gut content analysis of field-caught individuals (Pearson, 2009) suggests that they may be more predator than vegetarian; 88% of the collected individuals contained arthropod remains, but only 54% contained plant matter. Eating a diet rich in invertebrates should provide a sufficient amount of protein (see Fig. 1), but if invertebrate prey items are lean (i.e. low in energy), feeding on plant material (e.g. *Spartina* leaves) may be an effective strategy for *Conocephalus* to redress energy deficiencies, because generally *Spartina* has a lower protein–energy ratio compared with animal prey (see Fig. 1). The other advantage to feeding on *Spartina* is that it simultaneously limits over-ingestion of protein (especially when measured in terms of absolute amounts), and in some instances too much protein may become toxic (see Raubenheimer & Simpson, 1999; Simpson *et al.*, 2004; Raubenheimer *et al.*, 2005).

In the short-term *Conocephalus* may have some capacity to post-ingestively regulate protein intake, but animals that overeat nutrients in excess of requirements for an extended period of time often suffer reduced performance (e.g. Simpson *et al.*, 2004; Raubenheimer *et al.*, 2005). Interestingly, another omnivore, the German cockroach (*Blattella germanica* L.), provides an exception to this general overeating rule. Raubenheimer and Jones (2006) showed that, across a broad range of protein–carbohydrate concentrations, its survival was unaffected (Raubenheimer & Jones, 2006). Here the authors postulated that it adjusted to variations in the balance of ingested nutrients using physiological mechanisms associated with surviving long periods of famine. Cockroaches are opportunistic scavengers and extreme generalists that have the ability to use their fat body to store N, in the form of uric acid, and carbohydrates, in the form of lipids (Douglas, 1989). Cockroaches also have a number of paunches in the hindgut that house bacteria, which provide essential nutrients (Bourtzis & Miller, 2003). In contrast, *Conocephalus* are leaner than cockroaches with a less well developed fat body system and with no nutritional endosymbionts isolated from their alimentary canals (Nation, 2001).

Despite survival differences among treatments, no differences in growth were observed for individual *Conocephalus* that survived to the end of the 12-day experiment. Analysis of body lipid content revealed, however, that the protein–carbohydrate ratio of the diet significantly affected *Conocephalus* body composition. If growth is viewed in terms of lean mass (total mass – body fat), which places an emphasis on structural growth, the best diet for *Conocephalus*, in terms of combining survival and relative lean mass (total mass – lipid content), is the slightly protein-biased one (p50 : c30). That

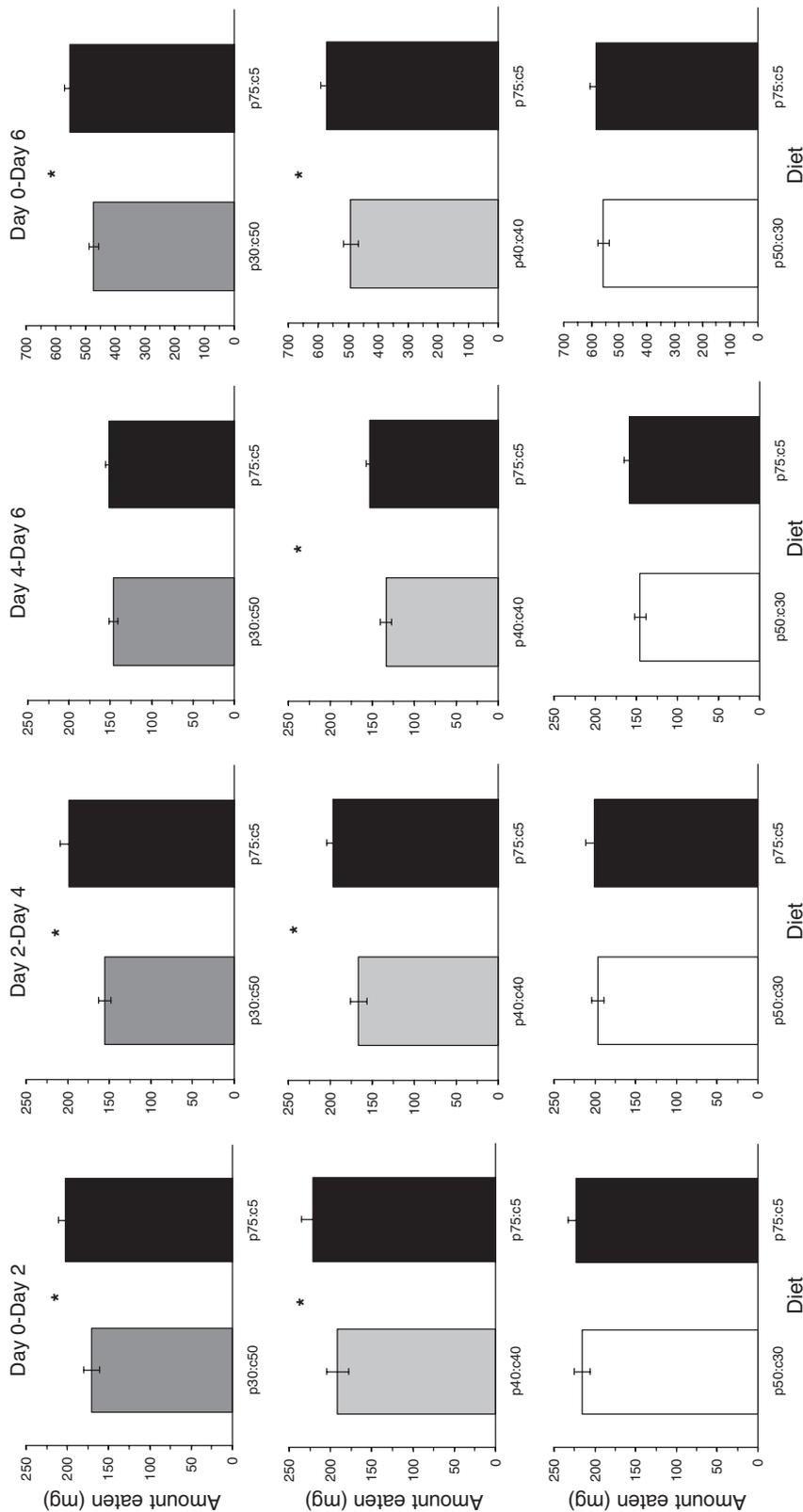


Fig. 4. Comparison of the mean diet eaten (\pm SE) for each of the four time periods (days 0–2, days 2–4, days 4–6 and days 0–6). Differences ($P < 0.05$) in the amounts consumed are denoted by (*).

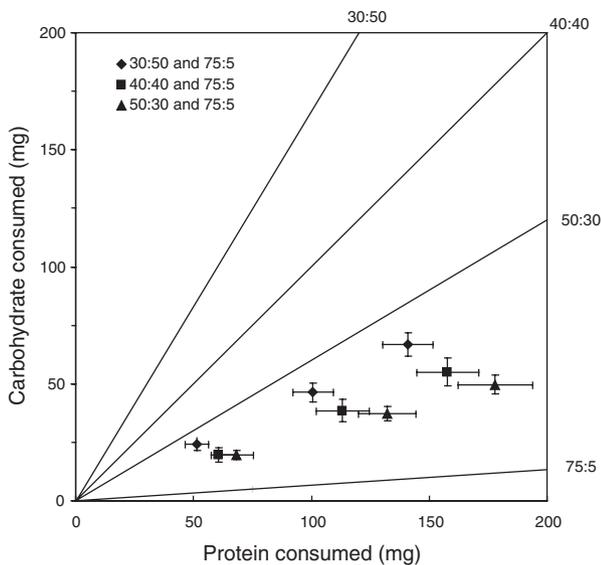


Fig. 5. Bivariate means of protein and carbohydrates consumed (\pm 95% CL) by *Conocephalus spartinae* when given one of three paired diets: (◆) 30:50 and 75:5, (■) 40:40 and 75:5 and (▲) 50:30 and 75:5. The first set of points in the series represents the amount consumed after the first 2 days. The second set of points is the total amount consumed after 4 days and the final set of points is the total amount consumed after 6 days. The dark lines represent the nutritional rails of the four diets as listed in the margin.

this particular diet is the best in the no-choice experiment for *Conocephalus* is interesting on two fronts. First, it has a similar protein–energy ratio to one of the most abundant prey items (planthoppers; see Fig. 1). Second, it is close (in terms of its nutrient-space position) to the protein–carbohydrate ratio that was self-selected in the choice experiment.

In the field *Conocephalus* can access a broad range of food types, with different nutrient compositions, and this at the minimum provides the opportunity to regulate their macronutrient intake. Results from our choice experiments reveal two key findings. First, *Conocephalus* is not a random feeder with respect to its macronutrient intake. We presented *Conocephalus* nymphs with three different food pairings, and when the balanced (40 : 40) or carbohydrate-biased (30 : 50) foods were paired with the highly protein-biased (75 : 5) food, a clear preference for the protein-rich food was observed over the entire experiment, and for each time period except the final one (days 4–6) where p40 : c40 was present. In contrast, no food preference was observed when p50 : c30 food was paired with p75 : c5 food. However, this does not rule out the possibility of nutrient regulation was occurring; here the protein–energy intake target would have been achieved by eating equally from among the two available food types. Nutrient regulation has been repeatedly observed in insect herbivores (reviewed by Behmer, 2009) and demonstrated in predaceous arthropods (Mayntz *et al.*, 2005; Pekar *et al.*, 2010), and we can now add a non-cockroach insect omnivore to the list.

The second key finding was that while *Conocephalus* nymphs self-selected a protein-rich diet, they did not tightly

regulate their protein–energy intake, as has been observed repeatedly in insect herbivores (reviewed by Behmer, 2009). *Post hoc* contrasts revealed that for each time period, none of the self-selected intake targets converged on a single point. Perhaps tight macronutrient regulation isn't essential if *Conocephalus* possess efficient post-ingestive physiological processes that allow compensation for differences in nutrient intake. Raubenheimer and Simpson (1993) showed that locusts, over the short-term (a single developmental stadium), could reach similar growth targets across a wide-range of protein–carbohydrate diets. In cases where carbohydrates are in excess, post-ingestive processes include respiring excess carbohydrates (Zanotto *et al.*, 1993, 1997) and/or converting carbohydrates to fat and storing them (Simpson *et al.*, 2002). Some insects can process excess N; for example, some orthopterans (e.g. *Locusta migratoria* L.) can metabolise excess protein and use amino acids as a source of energy via deamination (Raubenheimer & Simpson, 2003). It appears that *Conocephalus* can at least convert excess carbohydrates to fat, but we currently know little about the extent to which invertebrate predators or omnivores can produce energy via deamination. Alternatively, if excess protein cannot be used to generate energy, protein can be metabolised during digestion, and amino acids in excess of requirements can be voided during excretion (Zanotto *et al.*, 1993). However, the high mortality of *Conocephalus* on the heavily protein-biased diets suggests this is likely not an option.

As an omnivore, *Conocephalus* includes both plant and animal material in its diet despite large differences in macronutrient composition among dietary resources. In our short-term feeding experiments, *Conocephalus* flexibly accepted a wide range of artificial diets to maintain growth. However, our high protein, very low energy diet (p75 : c5) clearly shows that carbohydrates (energy) can be limiting for *Conocephalus*. Perhaps when energy is limiting (either because prey items are lean, or prey items are scarce), plants provide a readily available energy source, mostly in the form of digestible carbohydrates (simple sugars and starch). The apparent short-term nutritional flexibility of *Conocephalus* makes sense in the resource landscape found on the mid-Atlantic salt marsh where planthopper prey can reach outbreak numbers and plant quality is variable over space and time. *Conocephalus* can utilise these variable conditions by consuming available resources and, like generalist herbivores, consuming unbalanced foods when they are encountered because the probability of encountering a complementary food will be high (Raubenheimer & Simpson, 2003; Behmer, 2009).

For omnivores like *Conocephalus*, feeding on plants or prey may not represent an 'either/or' situation, but rather a nutritional continuum where they benefit by sampling their surroundings or feeding complementarily to meet their nutritional requirements. The degree to which an omnivore mixes its diet likely depends not on whether a plant or an animal itself is more nutritious, but rather how each, when combined, fulfil an omnivore's nutritional needs at that particular time. These needs, of course, can change over time depending on both the state of the omnivore (age, sex etc.) and the state of its environment (resource availability,

abiotic conditions, toxins, etc.). We propose that to more fully understand how omnivores affect population ecology, food-web dynamics, and biological control, it will be important to gain a better understanding of the functional significance of switching between plants and prey, how and the extent to which they regulate their food intake, and how in turn this regulation affects their fitness.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:

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Table S1. Constituents of four artificial diets fed to *Conocephalus*.

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