



Food mixing strategies in the desert locust: effects of phase, distance between foods, and food nutrient content

Brenda van der Zee^{1,2}, Spencer T. Behmer^{1,*} & Stephen J. Simpson¹

¹Department of Zoology and University Museum of Natural History, University of Oxford, South Parks Road, Oxford OX1 3PS, UK; ²Current address: Laboratory of Entomology, Wageningen University, 6709 PD Wageningen, The Netherlands; *Author for correspondence (E-mail: spencer.behmer@zoo.ox.ac.uk)

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Abstract

Food mixing strategies were compared in the cryptically coloured, relatively sedentary ‘solitarious’ and the highly mobile, conspicuously coloured ‘gregarious’ phases of the desert locust, *Schistocerca gregaria*. Based on phase related differences in behaviour and nutritional regulatory responses, we predicted that solitarious nymphs, compared to gregarious nymphs, would move less between nutritionally complementary foods, particularly as the distance between the foods increased. We manipulated the nutritional composition [protein (p) and digestible carbohydrate (c) content] of two foods in an experimental arena and varied the distance between the foods using a factorial experimental design. Results indicated that in general, solitarious nymphs showed greater fidelity to individual food dishes than did gregarious insects (i.e., they concentrated their feeding mainly on one dish). However, results also demonstrated that for both phases fidelity to a particular food dish increased as the distance between the dishes increased, and that the number of switches between dishes decreased with increasing distance. In the smallest arenas, though, gregarious nymphs switched more frequently between the two food dishes than solitarious nymphs, even when the two dishes contained the same, near-optimal food (p18:c24). When challenged by having the two dishes either placed furthest apart (2 m) or more divergent in nutritional composition (p29:c13 vs. p7:c35), insects of both phases regulated protein intake more strongly than carbohydrate intake, by eating more from the dish containing higher-protein food.

Introduction

Insect herbivores have been shown to be able to mix an optimal diet by selecting among foods that differ in their nutritional composition (Simpson & Simpson, 1990; Waldbauer & Friedman, 1991; Raubenheimer & Simpson, 1999). However, when mixing is not an option and only sub optimal foods are available, they must balance under-eating some nutrients against over-eating others and, as a result of this compromise, they may suffer performance costs (Raubenheimer & Simpson, 1999). A key question, therefore, is whether an insect herbivore should risk predation and other fitness consequences of moving and finding foods that are either balanced or nutritionally complementary, or whether it should remain feeding on a nutritionally

deficient food, and tolerate the associated costs of doing so. The solution to this dilemma will depend on several factors, including the extent of nutritional inadequacy in the present food, the mobility of the animal, the risk of predation in moving to an alternative food, and the chemical composition of, and distance between, alternative foods (Bernays et al., 1997; Lima, 1998).

The desert locust, *Schistocerca gregaria* (Forskål) (Orthoptera: Acrididae), provides an excellent system for investigating this issue since the same individual can exist in two forms (phases), depending on population density (Uvarov, 1977; Pener, 1991; Simpson et al., 1999). Solitarious phase nymphs are cryptically coloured (green or brown) and relatively inactive. They also behave cryptically, being repelled by

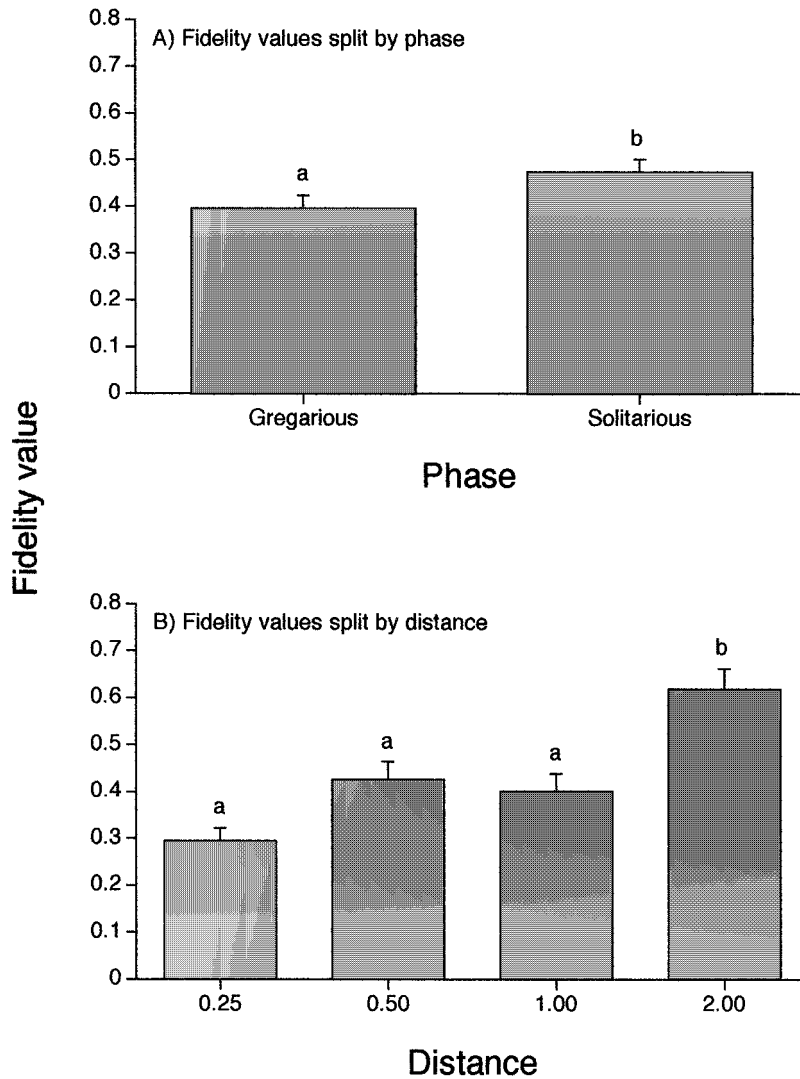


Figure 1. The mean (\pm s.e.) Fidelity value (see text) shown for locust phase (Panel A) and distance between food dishes (Panel B). Different letters above the bars indicate significant differences between the treatments.

other locusts and freezing when visually disturbed. Although they are potentially highly polyphagous, solitary locusts live in low-density populations in desert environments that are usually dominated by a small number of host plant species (Ghaout et al., 1991). In contrast, gregarious phase locusts are conspicuously coloured as nymphs (yellow, black, and orange), highly mobile, and adapted to living at high population densities. When in crowds, they form marching bands that can travel considerable distances (up to ca. 1000 m per day as final-instar nymphs) (Ellis & Ashall, 1957). Their conspicuous coloration may confer protection against vertebrate predators, particularly during the

initial stages of an outbreak, serving as an associatively learned stimulus when paired with toxic plant material in the insect's gut (Sword, 1999; Sword et al., 2000).

Being less mobile and more cryptic in behaviour and coloration, it might be predicted that solitary phase should show greater fidelity to a feeding site than gregarious nymphs. If so, they should be less likely to move between complementary foods as the distance between the sites is increased. Associated with being more sedentary, solitary nymphs employ a different nutrient regulatory strategy than gregarious nymphs, and recent work indicates that they are better

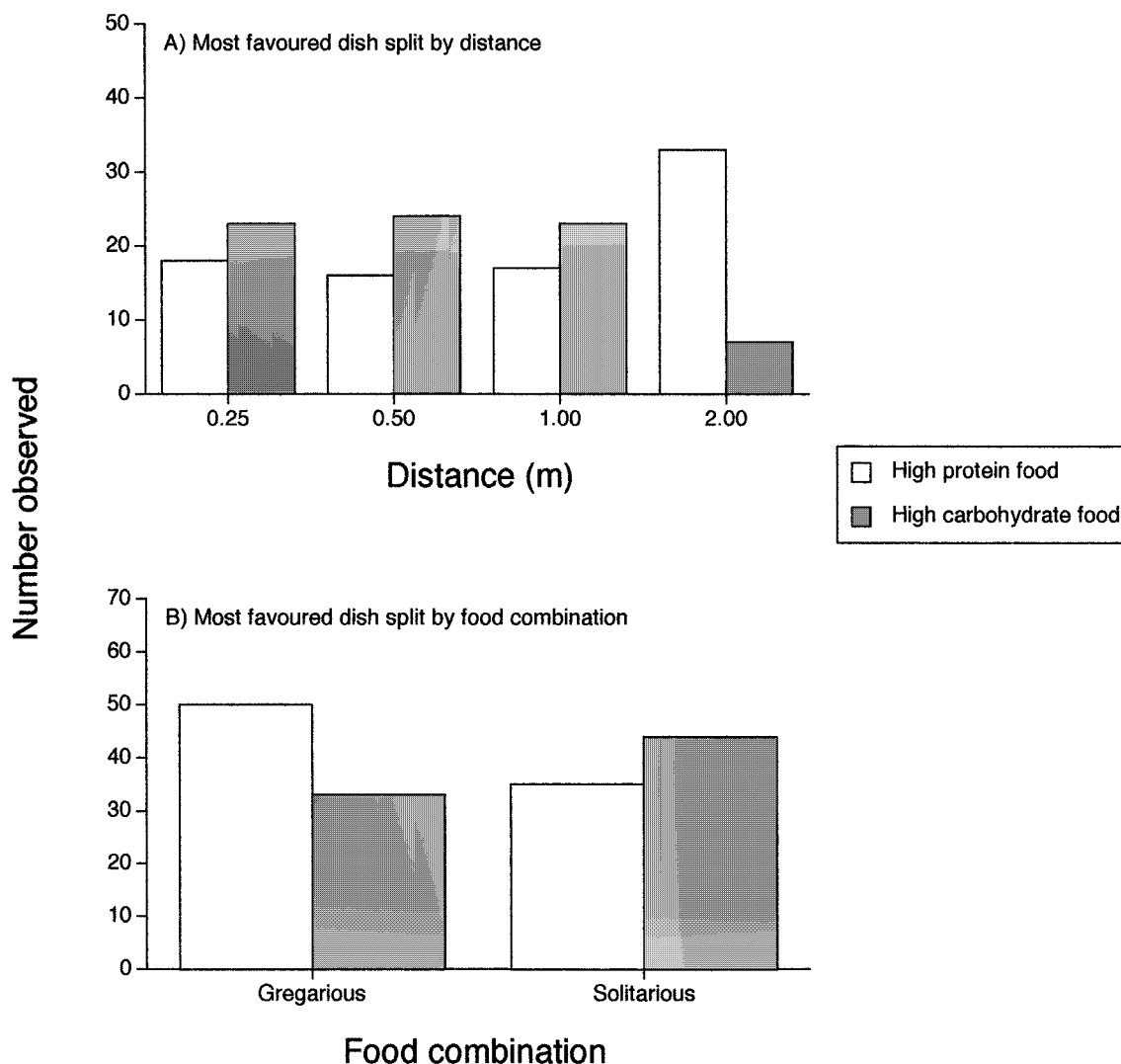


Figure 2. Data from treatments with nutritionally complementary foods in the arena, showing the number of locusts that ate most from the high protein food dish and the number that ate most from the high carbohydrate food dish. Panel (A) shows these numbers sorted by distance, while Panel (B) shows these numbers sorted by food combination.

able to tolerate nutritional imbalances that would result from limited movements between foods (Simpson et al., 2002). To test the predictions that solitary nymphs should switch less between food resources than gregarious nymphs, we employed a factorial experimental design where we manipulated the distance between two foods and the nutritional composition of the available foods.

Materials and methods

Insects and experimental chambers. Desert locusts, *Schistocerca gregaria*, were either crowd-reared for many generations (since 1983) (gregarious phase) or from the same inbred stock but solitary reared for three generations (solitary phase) in the Department of Zoology, University of Oxford, UK, according to the methods described in Roessingh et al. (1993). Both gregarious and solitary cultures were fed a diet of greenhouse-grown seedling wheat and wheat germ. Insects were kept at 29–31 °C under a L12:D12 regime. The solitary-reared nymphs have a character-

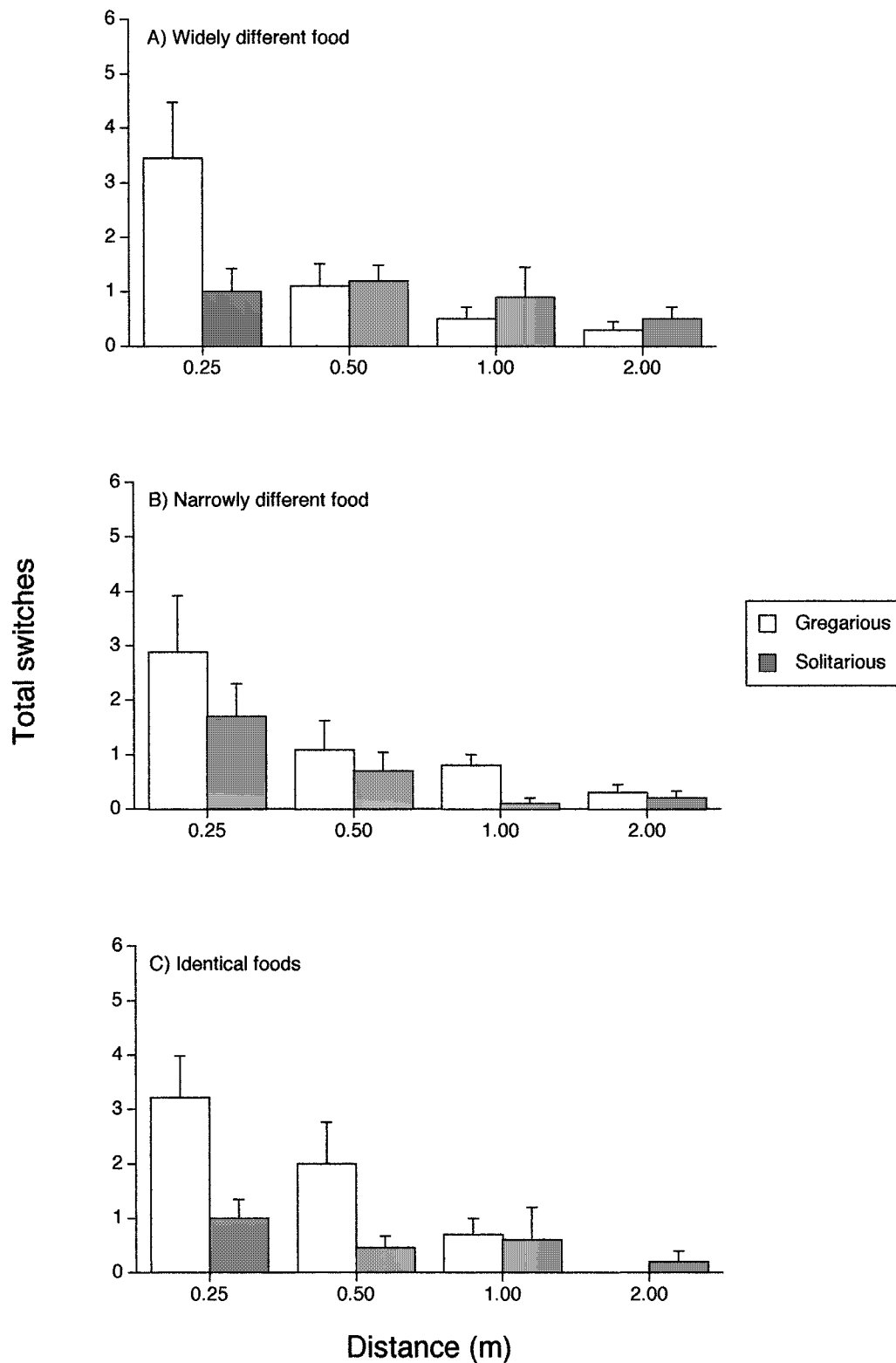


Figure 3. The mean (\pm s.e.) number of switches between food dishes observed over two 2-h observation periods for each of the four distances. Locusts were provided with one of three food combinations: (A) p29:c13 vs. p7:c35 (widely different), (B) p29.5:c18.5 vs. p12.5:c29.5 (narrowly different) or (C) p18:c24 vs. p18:c24 (identical foods).

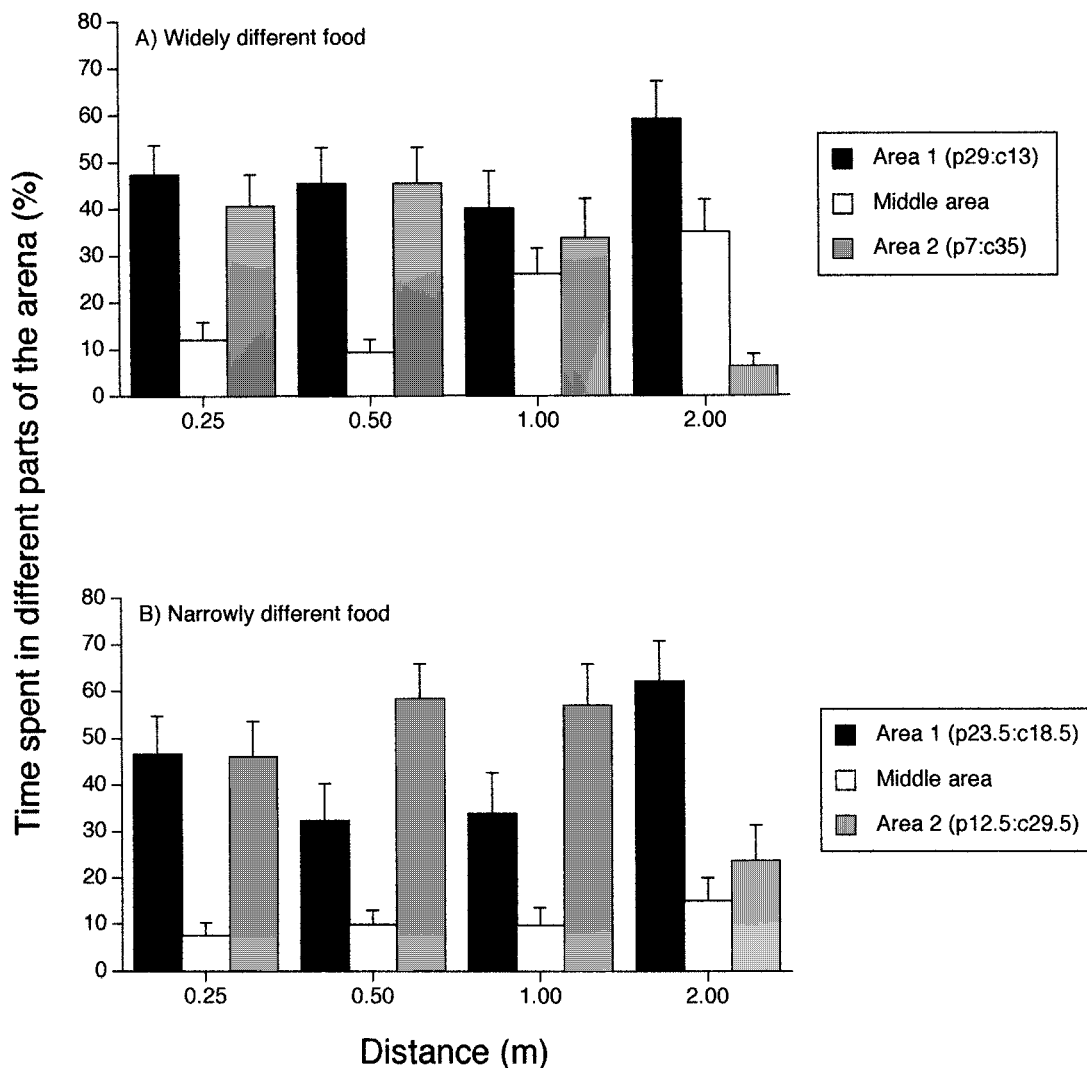


Figure 4. The mean (\pm s.e.) amount of time spent by locusts (as a percent) in different areas within the arenas (on or near the high-protein or high-carbohydrate food or somewhere in between the two foods) over two 2-h periods. Panel (A) shows the time spent in the three defined areas within the arena when the nutrient content of the two complementary foods differed widely while Panel (B) shows the time spent in the three defined areas within the arena when the nutrient content of the two foods was narrowly different.

istic green or brown colour, while the crowd-reared nymphs show a conspicuous colour pattern (see Simpson et al., 1999).

Nymphs of both sexes were collected from the cultures at ecdysis to the final nymphal stadium. After being weighed to ± 1 mg, locusts were placed singly into one of four different sized Plexiglas arenas [It is important to note that within the first 4 h of isolation partial behavioural solitarization occurs in initially gregarious locust nymphs. Thereafter the insects remain in a stable, significantly gregarized behavioural state for the rest of the stadium (Roessingh

& Simpson, 1994)]. All arenas were the same height (8 cm) and width (15 cm) but differed in length (0.25, 0.5, 1, or 2 m). At each end of the arenas we placed an aluminium perch for resting, a small plastic container ($7 \times 4 \times 2$ cm with two 1.5-cm holes in the top) filled with water for drinking, and a food dish [modified Petri dishes specifically designed to minimize spillage (Raubenheimer & Simpson, 1990)]. The sides of the arenas were covered with white paper to prevent locusts from seeing one another. All experiments were conducted at 29–31 °C under a L12:D12 regime.

Diets. Dry, granular chemically defined foods, similar to those developed by Dadd (1961) and modified by Simpson & Abisgold (1985), were made that varied in the ratio of protein (p) to digestible carbohydrate (c). Ratios (in % dry mass) were as follows: p29:c13, p23.5:c18.5, p18:c24, p12.5:c29.5, and p7:c35. A previous study had shown that for final instar solitary and gregarious nymphs of *S. gregaria*, the self-selected diet composition, which supports optimal performance, is p18:c24 (Simpson et al., 2002). The p29:c13 and p7:c35 foods were thus chosen as a pairing of individually imbalanced foods that were symmetrically complementary about this self-selected ratio. The p23.5:c18.5 and p12.5:c29.5 foods were also unbalanced, symmetrically complementary foods, but the difference in nutritional content of these two foods was not as extreme compared to the first pairing. All foods contained 54% cellulose powder and 4% essential micronutrients (salts, vitamins, cholesterol, and linoleic acid). Digestible carbohydrate consisted of a 1:1 mix of sucrose and white dextrin, while protein contained 3:1:1 casein:peptone:albumen.

Protocol. In total there were three food combinations: (1) p29:c13 with p7:c35 (widely different complementary food pairing), (2) p23.5:c18.5 with p12.5:c29.5 (narrowly different complementary food pairing), and (3) two dishes of p18:c24 (a diet close to that self-selected by these insects). On the day before the experiments were to start, the foods were added to the appropriate dishes and allowed to equilibrate to ambient room humidity levels (r.h. 30–40%) for approximately 24 h. They were then weighed to the nearest 0.1 mg and placed inside the arenas. After the locusts had been allowed to feed for three days both they and the foods were removed. The locusts were weighed and returned to their respective cultures, and the food dishes were allowed to re-equilibrate to ambient room humidity levels (ca. 24 h) before being reweighed. Approximately ten replicates of each treatment were run and in total 120 gregarious nymphs (58 males and 59 females) and 122 solitary nymphs (55 males and 67 females) were used.

On the last day of the experiment, day 3, observations were undertaken every 10 min for 2 h in the morning (from 0900h to 1100; lights-on at 0800) and 2 h in the afternoon (from 1500h to 1700; last 2 h of the experiment). For each individual we recorded whether it was less than one body length from one food dish or the other, or whether it was somewhere in between the two food dishes. The aim of recording this in-

formation was to measure the frequency of switching between the two food dishes and to determine whether locusts demonstrated fidelity for a particular defined area within the arenas. In total each individual was observed 26 times.

Statistics. Various measures of consumption and behaviour were analysed using the statistical packages SAS 6.12 (SAS Institute, 1985). For instance, ANOVA or ANCOVA was used to compare levels of fidelity, the frequency of switching between foods and mass gain. We measured fidelity using a Levene Index, which was calculated as follows:

$$LI = |(D1_{amt} - D2_{amt})| / (D1_{amt} + D2_{amt}),$$

where $D1_{amt}$ is the amount eaten from the first food dish and $D2_{amt}$ is the amount eaten from the second food dish. The vertical lines indicate the absolute value is being used. Values near 0 indicate no fidelity while values approaching 1 indicate strong fidelity to one of the two food dishes. To compare amounts eaten from the two dishes, protein and carbohydrate intake targets and locust position in the arenas, we used MANCOVA. The covariate used throughout the analyses was initial starting mass of the locusts. Where post hoc comparisons were performed, a Tukey test was used unless otherwise specified.

Results

Fidelity value. When we examined levels of fidelity to the food dishes, as measured by the Levene Index, we observed a significant difference between the two phases (ANOVA: $F_{1,215} = 4.37$, $P = 0.038$). Solitary phase locusts were found to have greater fidelity to one of their food dishes than gregarious phase locusts (Figure 1A). There was also an effect of distance between the foods on levels of fidelity to a particular food dish (ANOVA: $F_{3,215} = 13.08$, $P < 0.001$). As shown by a Tukey test, measures of fidelity were similar at 0.25, 0.5, and 1 m, but at 2 m the value was significantly greater compared to the smaller distances (Figure 1B). Fidelity, as measured by the Levene Index, was not affected by food combination and no significant two- or three-way interactions were detected.

Fidelity based on nutrient content. For this analysis we examined the two complementary food combinations, and recorded for each individual locust whether

more had been eaten from the high protein or high carbohydrate food dish. We then examined these data using weighted least squares methodology (the CATMOD procedure in SAS v. 6.12). Results showed that the only explanatory factors in the model that were significant were distance and food combination ($\chi^2 = 30.24$ with $P < 0.001$ and $\chi^2 = 4.36$ with $P = 0.037$, respectively). For locusts in the 2.0 m arenas, a very strong fidelity was shown towards the high protein food (Figure 2A). For locusts in the 0.25, 0.5, and 1.0 m arenas, however, a weak fidelity for the high carbohydrate food dish was shown. With respect to food combination treatments, locusts offered the widely differing food treatment showed fidelity towards the high protein food dish while locust from the narrowly differing food treatment showed a reverse trend, with fidelity towards the high carbohydrate food dishes (Figure 2B).

Switching. When all the three food treatments were kept in the analysis, a significant interaction between distance and phase was observed on the number of switches locusts made between the foods (ANOVA: $F_{3,215} = 5.63$, $P = 0.001$). Gregarious locusts in the 0.25 m arenas switched more than solitary locusts in the same arenas, but no differences in the number of switches by the two phases was observed in the other three arenas (Figure 3). No other two- or three-way interactions were found to be significant.

Locust position in the arenas with complementary foods. Behavioural observation data for time spent on or near the high protein food, the high carbohydrate food or in between the two foods shows that there was a significant distance effect (MANOVA: $F_{9,438} = 4.49$, $P < 0.001$) [It should be noted that for all MANOVA and MANCOVA analyses in this paper, we used Pillai's trace as our test statistic]. Contrasts demonstrate that where locusts spent their time (either on or near the high protein or high carbohydrate food or somewhere between the two foods) was similar in the 0.25, 0.5, and 1 m arenas (Figure 4). Locusts in the 2 m arenas, however, spent significantly more time near the high protein food and less time near the high carbohydrate food relative to locusts in the three smaller arenas. There were also significant differences between the two food combination treatments (MANOVA: $F_{3,144} = 5.48$, $P = 0.001$). Relative to the narrowly differing foods, locusts offered the widely different foods spent more time near the high protein food and less time near the high carbohydrate

food (Figure 4A). Locusts offered the narrowly differing food spent more time near the high carbohydrate food (Figure 4B). There was no significant effect of phase on where locusts spent their time in the arenas (MANOVA: $F_{3,144} = 1.12$, $P = 0.342$).

Consumption based on food type (complementary treatments). When consumption of the two food types (high protein food and high carbohydrate food) was compared we found a significant distance (MANCOVA: $F_{6,290} = 6.16$, $P < 0.001$) and food combination (MANCOVA: $F_{2,144} = 13.00$, $P < 0.001$) effect but no phase effect (MANCOVA: $F_{2,144} = 0.354$, $P = 0.703$). Results demonstrated that greater amounts of high protein food and lesser amounts of high carbohydrate food were eaten in the 2 m arenas compared to the 0.25, 0.5, and 1.0 m arenas (Figure 5). With respect to the two food combination treatments being examined, locusts offered the widely differing treatment ate more high protein food and less high carbohydrate food than did locusts in the narrowly differing treatments, which ate more from the high carbohydrate food (Figure 5A & 5B). There were no significant two- or three-way interactions but locust starting mass, when used as a covariate, was significant (MANCOVA: $F_{2,144} = 22.34$, $P < 0.001$). In general, heavier locusts ate more than lighter locusts.

Effects on protein and carbohydrate intake (complementary treatments). A bi-coordinate plot of protein and carbohydrate intake is shown in Figure 6. Results indicate that protein and carbohydrate intake were significantly affected by distance (MANOVA: $F_{6,290} = 5.81$, $P < 0.001$) and food combination (MANOVA: $F_{2,144} = 14.11$, $P < 0.001$). Contrasts revealed that the intake reached by locusts from the 2 m arenas differed significantly from that of locusts from the 0.25, 0.5, and 1 m arenas, but when the latter three distances were compared to one another, no differences were found. When the two food combinations were compared, it was shown that similar amounts of protein were ingested but that a smaller amount of carbohydrate was ingested on the widely differing treatment compared to the narrowly differing treatment.

Performance effects. All insects survived across the experimental period. With respect to mass gain, we found no differences for any of the main effects or interactions, although the covariate, starting mass, was again significant (ANCOVA: $F_{1,214}$, $P < 0.001$) with

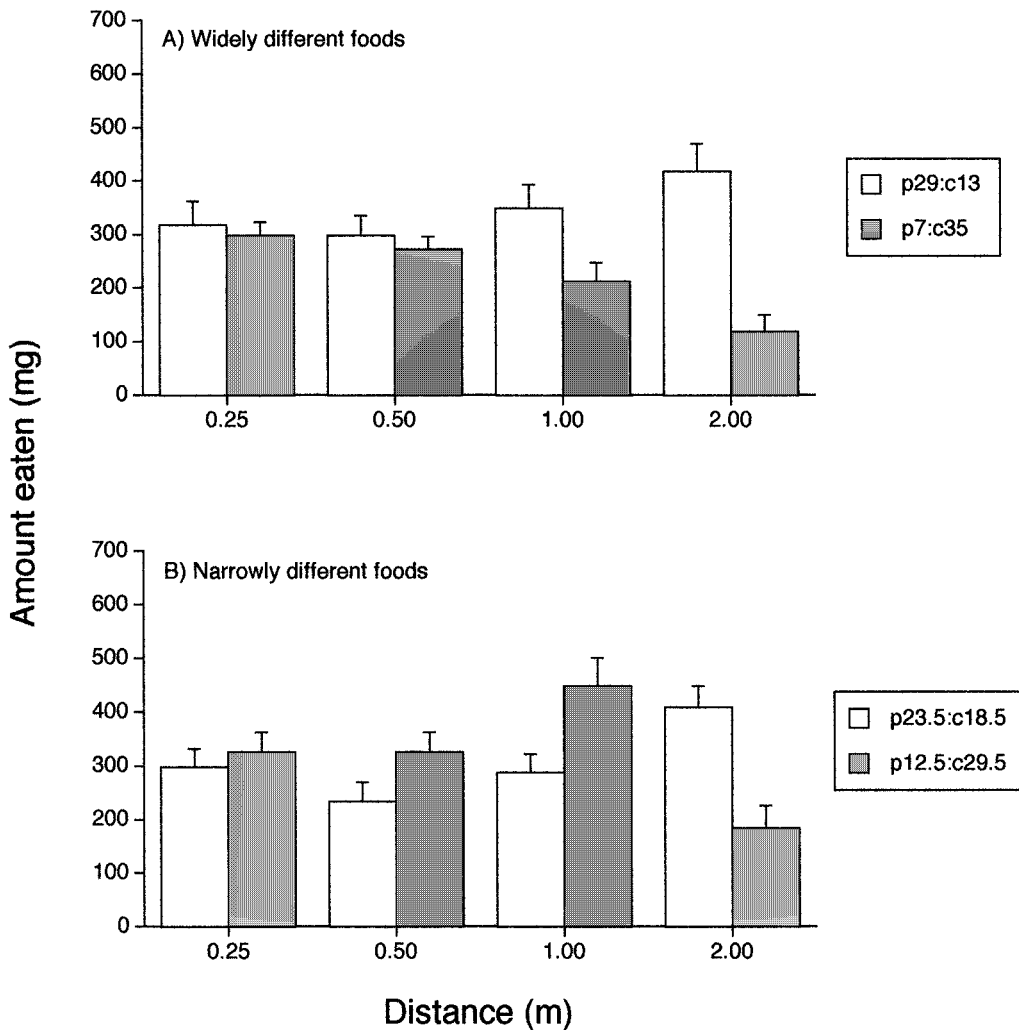


Figure 5. The mean (\pm s.e.) amount of high-protein and high-carbohydrate food eaten. Panel (A) shows the amounts eaten when the nutrient content of the two foods differed widely (p29:c13 vs. p7:c35), while Panel (B) shows the amounts eaten when the nutrient content of the two foods was narrowly different (p23.5:c18.5 vs. p12.5:c29.5).

larger locusts tending to gain greater amounts of mass than smaller ones.

Discussion

Our initial predictions were partially met by the results of the present experiments. Solitary nymphs showed greater fidelity to a food dish than did gregarious nymphs. Associated with this, gregarious nymphs switched between food dishes more frequently than did solitary nymphs when food dishes were close together (25 cm). However, as the distance between the dishes increased, both phases showed an increas-

ing fidelity for one food dish over the other and the number of switches decreased.

It was predicted that gregarious locusts should switch more frequently between dishes than solitary nymphs on the basis of known differences in their behaviour and nutritional ecology. Gregarious nymphs are conspicuously coloured and more active than their cryptically coloured, solitary counterparts. They are highly mobile and actively aggregate, demonstrating marching behaviour (Kennedy, 1939; Ellis, 1951; Roffey & Popov, 1968; Simpson et al., 1999). In a recent study (Simpson et al., 2002) it was found that the two phases of *S. gregaria* differ in their nutritional responses. When provided with pairs of nu-

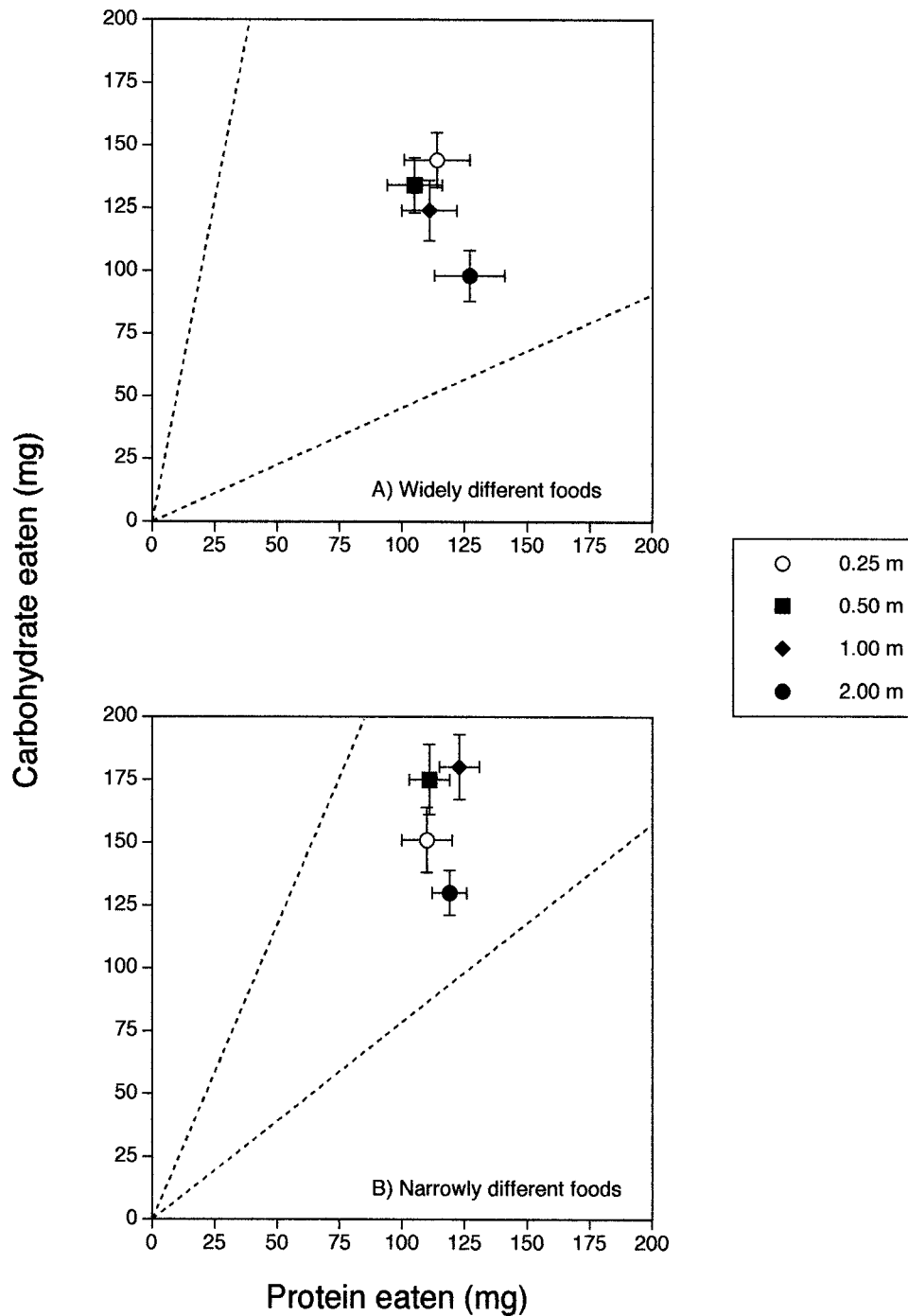


Figure 6. Bivariate means (\pm s.e.) of protein and carbohydrate intake for locusts given (A) two dishes of food that were widely different, and (B) two dishes of food that were narrowly different in composition. The dashed lines indicate the 'rails' of the available foods in the arenas.

tritionally imbalanced but complementary foods, both phases regulated their intake of protein and carbohydrate to a similar point (intake target). However, when confined to single foods that were of unbalanced pro-

tein to carbohydrate ratio, gregarious nymphs ate more than did solitary nymphs but converted ingested nutrients to growth with lower efficiency. These contrasting nutritional responses were hypothesised to be

adaptations to the different degree of nutritional heterogeneity experienced in the field by the two phases. Given their cryptic lifestyle, solitary insects should switch less and utilise nutrients more efficiently, while the highly mobile, gregarious insects should eat larger amounts of imbalanced foods and switch more frequently, discounting the costs associated with eating an imbalanced food against the higher expectation of encountering a complementary food in the future (Simpson et al., 2002).

Interestingly, a higher level of switching by gregarious than solitary nymphs was evident when the two dishes were 25 or 50 cm apart, even when the dishes contained the same type of near-optimal food (p18:c14). This result suggests that switching was not solely driven by the need to balance nutrient intake. Such 'compulsive' switching has been proposed to occur in conspicuous, chemically protected acridids (Raubenheimer & Bernays, 1993; Chambers et al., 1996), while more cryptic species appear to switch less frequently or have a narrower host range (Otte & Joern, 1977; Joern et al., 1986).

The differences in switching between the two phases disappeared as the distance between food dishes increased, with both phases concentrating their feeding on a single dish, moving little between dishes, and spending most of their time resting close to the favored food dish. The lack of difference between the two phases at these greater distances probably results from the insects being kept alone in the experimental chambers. Gregarious nymphs partially solitarise in their behaviour when isolated, becoming less active (Roessingh & Simpson, 1994). This partial behavioural phase change occurs over the first few hours of isolation, after which they remain in this transitional state until the end of the stadium, with further solitarisation requiring continuing isolation for several stadia. Such a response makes adaptive sense. Feeding and travelling between food resources entail heightened exposure to natural enemies (Bergelson & Lawton, 1988; Bernays, 1997; Hutchings et al., 2000). A single, conspicuously coloured gregarious nymph is likely to be more apparent than a cryptically coloured solitary insect, yet is not protected by being a member of a large aggregation.

A common feature of the feeding behaviour of both phases was that when the dishes were furthest apart (2 m), nymphs concentrated feeding on the dish containing higher protein food. At 1 m apart, more was eaten from the higher carbohydrate dish if the two foods were narrowly different in composition

(p23:c18.5 vs. p12.5:c29.5), but more was eaten from the higher protein dish when the foods were widely different (p29:c13 vs. p7.c37). At closer distances, a similar amount was consumed from both dishes. As a consequence, as is evident in Figure 6, when challenged by having the two dishes either placed further apart or more divergent in nutritional composition, insects regulated protein intake more strongly than they did their consumption of carbohydrate. These results are consistent with earlier research on locusts, showing stronger regulation of protein than carbohydrate intake (Simpson & Abisgold, 1985; Raubenheimer, 1992), and perhaps reflects the fact that while protein may be deaminated and used as a substitute for carbohydrate, the reverse is not the case.

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