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An adaptive benefit of facultative coprophagy in the German cockroach *Blattella germanica*

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Abstract. 1. A possible adaptive benefit of coprophagy was investigated in nymphs of the German cockroach *Blattella germanica* (L.).

2. Newly ecdysed first instars, given no source of food other than conspecific faeces, survived significantly longer than first instars deprived of faeces. The faeces of adult males and females may be of different quality, however, because nymphs given female faeces were more likely to moult into the second stadium than nymphs given male faeces.

3. In contrast to first instars, second instars provided adult faeces survived only slightly longer than starved counterparts. Faecal feeding is therefore stage-specific, as is the benefit derived from it.

4. The relationship between the nutrient composition of faeces and the survival of nymphs was also examined. First instars fed the faeces of adults that had been maintained on a high (50%) protein diet, died more slowly than first instars fed the faeces of adults that had been maintained on medium (22.5%) and low (5%) protein diets. Chemical analysis of faeces showed that the concentration of protein in adult faeces increased with the level of protein in the diet. Moreover, food choice assays showed that first instars, unlike adults, ingested more of the high-protein diets.

5. These data support the idea that coprophagy is a stage-specific adaptive behaviour that permits first instars to moult into the second stadium with minimal foraging.

Key words. *Blattella germanica*, cockroach, coprophagy, nutrient flow, survival analysis.

Introduction

Faecal consumption, or coprophagy, is a behavioural trait shared by many animal species, including mammals (e.g. mice, rats, guinea pigs, and rabbits; Hintz, 1969; Giovannetti, 1982; Ebino *et al*., 1988) and arthropods. In some insect species, this behaviour is obligatory whereas in others it is facultative. For instance, many dung beetle larvae feed exclusively on vertebrate excrement (Halffter & Matthews, 1966; Hanski & Cambefort, 1991) whereas flea larvae feed not only on the faeces of conspecific blood-fed adults but also on animal dander and hair (Bacot & Ridewood, 1914; Silverman & Appel, 1994). In obligatory coprophages, the adaptive benefit of faecal feeding is obvious; the faeces provide all that is necessary to sustain development and reproduction. In facultative coprophages, however, the benefit of faecal feeding may be less evident but is no less significant. Insects, for example mosquito larvae (Nilsson, 1983), can supplement their normal diet by obtaining nutrients from faeces. Moreover, insects can acquire micro-organisms from faeces that aid in nutrient utilisation. Some insects must do so in order to survive, in particular xylophagous insects that gain cellulose-digesting symbionts from conspecific faeces or hindgut exudates (Cleveland, 1925).

The German cockroach *Blattella germanica* (L.) is an important indoor pest with significant aesthetic, economic, and

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public health impacts. An investigation on the insecticidal properties of hydramethylnon showed that German cockroach nymphs consumed conspecific faeces. Silverman *et al*. (1991) traced ingested radio-labelled hydramethylnon from adult males and females to nymphs in laboratory cages. They concluded that nymphal mortality in these cages resulted from nymphs ingesting the insecticide-laden faeces of adults. This was later confirmed by Kopanic and Schal (1997), who found that first instars denied access to a toxic bait died when adults in the same cage fed on this bait. Moreover, Kopanic and Schal (1999) showed that a dye incorporated into faeces could later be recovered from the internal homogenates of first instars given access to the faeces.

The German cockroach aggregates in clusters composed of nymphs and adults of all ages. This spatial and temporal overlap of relatively sedentary neonates with older, more mobile nymphs and adults might favour facultative nutrient and symbiont exchange through coprophagy. The German cockroach may therefore prove a useful model in studies of nutrient flow in a gregarious, non-eusocial insect species. The aim of the study reported here was to determine whether nymphs derived a survival benefit from the ingestion of faeces and, if so, to determine how faeces promoted survival.

Materials and methods

Insects and rearing conditions

The *B. germanica* used in most experiments were from a laboratory colony obtained originally from American Cyanamid (Princeton, New Jersey). Colony cockroaches were provided water and Purina rat chow no. 5012 (Purina Mills, St Louis, Missouri) *ad libitum* and kept at 27 ± 0.5 °C under variable ambient humidity and a LD 12 : 12 h photoperiodic regime. Experimental cockroaches were maintained under similar conditions but were usually deprived of rat chow.

Experimental design

In experiments examining the effect of faeces on survival, nymphs were maintained in 150×25-mm Petri dishes that either contained faeces (experimental treatment) or did not (controls). Faeces-littered Petri dishes were prepared by confining 20 adult males or females in them for 6–7 days. The males were 10 days old when placed in the Petri dishes, whereas the females were 1 day old; both stages eat and therefore defecate maximally (Cochran, 1983; Hamilton & Schal, 1988). All adults were provided with water in cotton-stoppered tubes and rat chow in 25-mm diameter stainless steel planchettes. The planchettes were placed in the centre of 60×15-mm Petri plates, which caught spilled food and thereby prevented contamination of faeces with rat chow. After removing the insects, water tubes, planchettes, and small Petri plates, 20 neonates or newly moulted second instars were placed into each of 10 large Petri dishes, along with fresh water. Insects were thereafter inspected daily for mortality and removed and discarded on the day they died. Ten control treatments, in which nymphs were provided with water but no faeces, were run simultaneously.

The neonates used in some experiments were the offspring of females that had been collected in single-family dwellings in north-east North Carolina, U.S.A. At the time of their collection, the females were carrying oothecae. Within 24 h of being brought into the laboratory, the females were placed alone in 100×25-mm Petri dishes containing rat chow and water and monitored daily for nymphal hatch. Only nymphs that hatched within 3 days of their mother being brought into the laboratory were used. Newborns of a single mother were partitioned into two treatments, one in which they were given male or female faeces, the other in which they received neither. This design controlled for genetic, age-related, and nutritional differences among mothers. All nymphs were provided with water, and their mortality was recorded at 12- or 24-h intervals until the end of the experiment.

Manipulation of faeces composition

To prepare faeces that differed in composition, adult females were fed three different artificial diets of varying protein content (Table 1). All dietary ingredients were obtained from Bio-Serv (Frenchtown, New Jersey). Groups of 20 females were reared for 6 days in 150×25-mm Petri dishes containing water and one of the diets. To ensure that the faeces excreted by the females were the end-products of the artificial diets, females were starved for 24 h before they were placed in Petri dishes with the diets. After the adults and food were removed, 20 neonates were placed in each Petri dish along with a water tube. They were thenceforth monitored daily for mortality.

Analysis of diets and faeces

The lipid, carbohydrate, and protein contents of each experimental diet, and of the faeces that females produced after feeding on each diet, were determined. To obtain faeces for analysis, newly eclosed adult females were starved for 48 h,

Table 1. Compositions of three defined diets, by per cent.

Ingredient	High protein (50%)	Medium protein (22.5%)	Low protein (5%)
Soy protein (90%)	55.6	25	5.6
Dextrin	18.8	49.4	68.8
Corn syrup	10	10	10
Alphacellulose	5	5	5
Soy oil	5	5	5
Wesson's salt mix	4	4	4
Cholesterol	1	1	1
Vanderzant vitamins	0.6	0.6	0.6

fed an artificial diet for 4 h, then moved to a clean Petri dish devoid of food. For each diet, a 0.5–1 g sample of faeces was collected, and chemical analyses were conducted on small amounts of faeces taken from these samples. Lipids were extracted from food and faeces in chloroform–methanol–water (1:1:0.9) according to Bligh and Dyer (1959). Total lipid was determined colorimetrically using the vanillin reagent (Goldsworthy *et al.*, 1972), with cholesterol as a standard. Total sugar was determined using the anthrone assay with glucose as a standard (Roe & Dailey, 1966). A preliminary attempt to quantify protein yielded low values, which indicated that many of the proteins were relatively insoluble in water. Proteins were therefore solubilised in 1 N NaOH, and total protein was determined using the Bio-Rad assay (Bradford, 1976), with soy protein (Table 1) as a standard. Nitrogen analysis was performed using a Perkin-Elmer PE2400 CHN elemental analyser (Norwalk, Connecticut). Calorimetry was conducted on 1 g aliquots of diet and faeces using a 1241 oxygen bomb calorimeter (Parr Instrument Corporation, Moline, Illinois).

Dietary preferences of different life stages

Dietary preferences of adult males, adult females, and newly hatched nymphs were determined in two-choice assays. Twenty newly eclosed adult males or females or 50 newly hatched nymphs were placed in a Plexiglas® cage ($19 \times 14 \times 9.5$ cm) and provided with water, a cardboard shelter, and a feeding tray. The feeding tray was a rectangular block of Plexiglas® ($7 \times 5 \times 1.5$ cm), the two lengths of which were cut at 45° angles to facilitate access of insects to a pair of diet cups located in circular holes cut into the top surface of the station. The symmetrical design of the tray eliminated feeding bias based on food position. Insects were simultaneously offered equal amounts of a high-protein (55% protein, 30% carbohydrate) and low-protein (5% protein, 70% carbohydrate) diet. Food intake was determined by weighing each diet cup every 24 h over a 3-day period.

Analysis of survival data

In all experiments, survival of nymphs in different faeces treatments was compared with survival in a faeces-deprived control group. The results were summarised by plotting Kaplan–Meier estimates of S(t), the probability of survival to time t, against time (Parmar & Machin, 1995). The survival curves of two groups of insects were compared using the log-rank test, modified for interval censoring (Whitehead, 1992); the curves of three or more groups were compared using Cox's proportional hazards model using an exact likelihood method (Allison, 1995). The Wald test was used to determine whether coefficients of variables were significant, differing from zero. The likelihood ratio test (Parmar & Machin, 1995) was used to determine whether a model with regression coefficients described the survival data better than did a null model without coefficients.

Hazard ratios were obtained by exponentiating regression coefficients in Cox models. An important assumption of a Cox model is that the hazards of all groups in the model are proportional through time (Parmar & Machin, 1995). Proportionality of hazards was assessed by plotting the complementary log transformation of the survival function, $\ln\{-\ln[S(t)]\}$ against the natural logarithm of time for each group incorporated into the model. The hazards of the different groups were considered proportional if their complementary log plots were parallel, or nearly so.

Kaplan–Meier estimates of survival probabilities were determined using PROC LIFETEST (SAS Institute Inc., 1990) in SAS® version 6.12 for the personal computer. Cox modelling was carried out using PROC PHREG in SAS® (SAS Institute Inc., 1996). All other statistical calculations were performed using Microsoft® Excel 98 (Microsoft Corporation, Redmond, Washington). In the text, standard error of the mean (SEM) is given with all means.

Results

Coprophagy postpones the death of starved nymphs

Survival of starved nymphs given no faeces and nymphs with access to adult male or female faeces was determined and subjected to Kaplan–Meier estimates of the probabilities of nymphs in different treatments surviving to any day of the experiment. The resulting step graphs showed that a newly hatched nymph provided either male or female faeces had a ~90% probability of surviving for 10 days and a >70% probability of living for ⩾2 weeks (Fig. 1a). In contrast, all nymphs without faeces were dead by day 10. Nymphal death

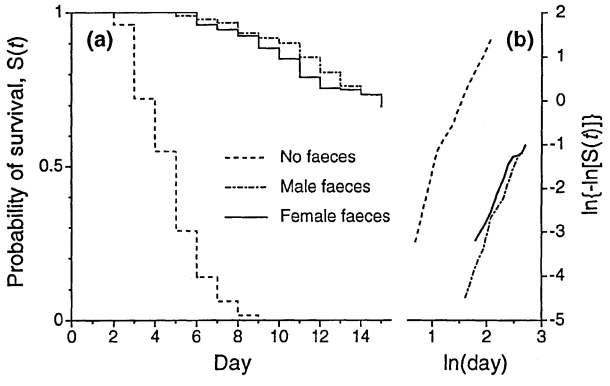

Fig. 1. Survival of first instars on adult male or female faeces. (a) Step plots show Kaplan–Meier estimates of the probability of a nymph surviving to each of the first 15 days after hatch. The values along the *X*- and *Y*-axes in (a) were transformed to yield complementary log plots (b). Twenty newly hatched first instars were placed in Petri dishes containing water and either no faeces or adult male or female faeces, and mortality was recorded daily. The results of 10 replicates, 20 nymphs each, were pooled before calculation of Kaplan–Meier estimates.

rates in the different treatment groups were compared using proportional hazards modelling. The hazards, or instantaneous rates of death, of nymphs with or without faeces were proportional throughout the 15 day experiments (Fig. 1b). The final model contained two regression coefficients (Table 2), both significant (Wald test, $P < 0.001$), describing the effect of male and female faeces on survival. Exponentiation of these coefficients yielded hazard ratios (Table 2), which showed that nymphs provided with male or female faeces died at 0.016 and 0.017 times the rate of nymphs without access to faeces (Table 2). Nymphs without faeces therefore died about 60-fold faster than those with faeces. The hazard ratios and their 95% confidence intervals were nearly identical, indicating that the rates of death of nymphs given male and female faeces did not differ.

In a separate experiment, nymphs were examined beyond day 15, and, ultimately, differences were found in the survival of nymphs provided different types of faeces. On day 24, only $32.5 \pm 4.0\%$ ($n = 10$ replicates of 20 nymphs) of nymphs given male faeces remained alive, compared with $58.5 \pm 3.2\%$ ($n = 10$ replicates of 20 nymphs) of nymphs given female faeces. Nymphal development was also affected by faeces type. During the entire experiment, only $8.0 \pm 2.8\%$ of nymphs given male faeces moulted into the second stadium, compared with $54.5 \pm 6.1\%$ of nymphs given female faeces.

To determine whether these findings were relevant to feral cockroaches, experiments were conducted with the offspring of field-collected females, gravid at the time of their collection. The newborns of individual females were partitioned into two groups, one in which they received male or female faeces, the other in which they received neither. Kaplan–Meier plots (Fig. 2) showed that the patterns of death of the faeces-provided and faeces-deprived nymphs were similar to those of laboratory-reared nymphs (Fig. 1). Moreover, in all cases, the nymphs given faeces survived significantly longer than those deprived of faeces (log-rank statistic; range of χ^2 values 20.12–42.87, 1 d.f., $P < 0.001$). These data suggest that first instars in their natural setting would gain a survival benefit from ingesting faeces, particularly when alternative food sources are scarce or far from their shelter.

Kaplan–Meier plots (Fig. 3) and proportional hazards modelling (Table 2) showed that second instars lived longer, but only slightly so, when given faeces. The hazards of the treatment groups were deemed sufficiently proportional in the first 15 days of the second stadium (Fig. 3) to use Cox modelling. The two regression coefficients in the model were highly significant (Wald test, Table 2), but the hazard ratios derived from these coefficients were substantially larger than the corresponding ratios obtained with first instars (Table 2). Second instars given male or female faeces died at about 60% of the rate of nymphs without faeces. To rule out the possibility that nymphs were given insufficient faeces to have an effect on their survival, the amount of faeces given to nymphs was increased four-fold. The survival of these nymphs was no better than that of nymphs given the standard amount of faeces (R. J. Kopanic, unpublished).

Effect of faecal nutrient composition on survival of first instars

First instars given faeces not only survived longer but grew. It was therefore reasonable to posit that nymphs were gaining nutrients from faeces. To test whether faecal nutrients were responsible for the prolonged survival of faeces-fed nymphs, the nutrient contents of faeces were manipulated and the effects of these changes on nymphal survival were examined. To obtain faeces of variable nutrient quality, adult females were fed three diets differing only in protein and carbohydrate content (Table 1). The chemical compositions of the diets, and of the faeces produced by females while consuming the diets, were analysed. In general, dietary macronutrient levels (Table 3) were as expected (Table 1), and slight deviations from the expected were probably due to the unknown portion of the soy protein mixture, which was 90% protein by weight. These results showed the adequacy of the analytical procedures

Table 2. Cox's proportional hazards models and hazard ratios (HR).

Model†	Stadium	Source of faeces‡	Regression coefficient, b	SE of b	Wald statistic $\chi^2 = (b/\mathrm{SE})^2$	P-value	HR = e^b	95% CI of HR
A	First	Male	−4.134	0.245	286.00	<0.0001	0.016	0.010–0.026
		Female	−4.103	0.240	292.56	<0.0001	0.017	0.010–0.026
B	Second	Male	−0.490	0.144	11.59	0.0007	0.612	0.462–0.812
		Female	−0.465	0.145	10.34	0.0013	0.628	0.473–0.834
C	First	Low protein	−1.289	0.154	70.35	<0.0001	0.275	0.204–0.372
		Medium protein	−1.247	0.153	66.02	<0.0001	0.287	0.213–0.388
		High protein	−2.287	0.176	169.30	<0.0001	0.102	0.072–0.143

†Likelihood ratio tests showed that the regression coefficients improved the fits of models A ($\chi^2 = 565.96$, 2 d.f., $P < 0.001$), B ($\chi^2 = 13.87$, 2 d.f., $P = 0.001$), and C ($\chi^2 = 173.87$, 3 d.f., $P < 0.001$).

‡In models A and B, the faeces were obtained from adult male and female cockroaches that had been fed rat chow, whereas in C the faeces were obtained from adult females that had been fed one of three defined diets (Table 1) containing 5% (low), 22.5% (medium), or 50% (high) protein.

used to measure substrate lipid, carbohydrate, protein, and nitrogen content.

Although the faeces resulting from the three diets were relatively iso-caloric (Table 3), the faeces composition was determined by the diet that females ate. As dietary carbohydrate content increased from 33.4 to 76.1%, so did the percentage of sugars in the faeces (Table 3). Faecal protein content also varied positively with its level in the diet and the faeces of females fed a high-protein diet contained almost six-fold more protein than did the faeces of females fed a low-protein diet. Faecal lipids varied, but only two-fold across the diets. In light of their protein content, the faeces contained much more nitrogen than would be expected, probably due to non-proteinaceous, nitrogen-containing compounds, mainly ammonia, in the faeces (Cochran, 1985).

Kaplan–Meier estimates of survival probabilities showed clearly that first instars survived longest on high-protein faeces, with 89% surviving to day 10 (Fig. 4). The survival patterns of insects on the medium- and low-protein diets were similar, with 57 and 55% respectively surviving to day 10. Faeces-deprived control nymphs died earlier, with just 11% surviving to day 10. The hazards of the four groups were

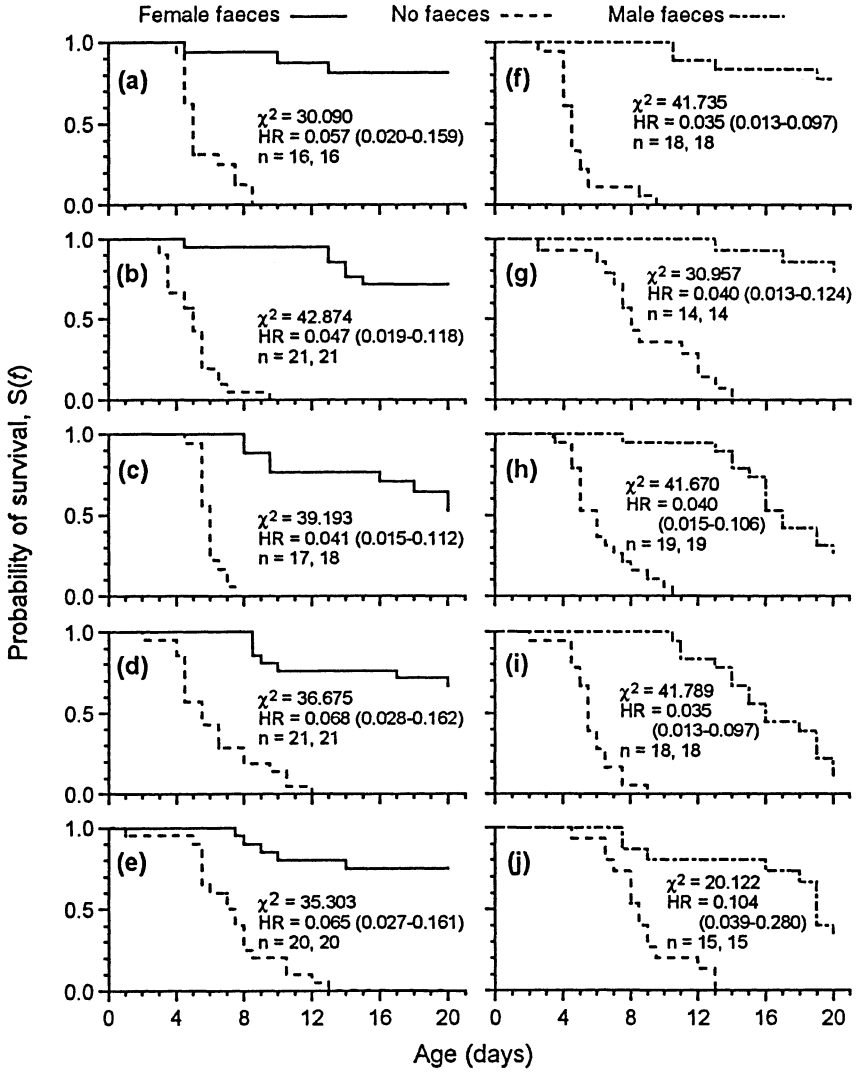

Fig. 2. Survival of the offspring of field-collected females, gravid at the time of their collection. Nymphs in (b, c), (e–g), and (i, j) were from mothers collected in the same home, (a) and (h) were from a second home, and (d) from a third. The number of nymphs in each group is shown, the first number representing the faeces-provided group, the second the faeces-deprived group. Each line in a graph shows Kaplan–Meier estimates of the probability of a nymph surviving to any of the first 21 days after hatch. Chi-square values (1 d.f.) were calculated using the modified log-rank test; all values were significant ($P < 0.001$). A hazard ratio (HR), along with its 95% confidence interval, is shown in each graph. The hazard ratio represents the mortality rate of nymphs in the faeces-provided group relative to that of nymphs in the control group.

reasonably proportional to the end of the experiment (Fig. 4), and nymphal death rates showed that first instars given high-protein faeces died at about one-tenth the rate (hazards ratio = 0.102; Table 2) of nymphs reared without faeces. Nymphs provided low-protein (hazards ratio = 0.275) or medium-protein (hazards ratio = 0.287) faeces died nearly three-fold faster than nymphs given high-protein faeces, but still more slowly than nymphs not provided with faeces. These results show that diet influenced faecal quality, which in turn affected nymphal survival. Moreover, they suggest that faecal protein may be the chief factor influencing nymphal survival in these tests.

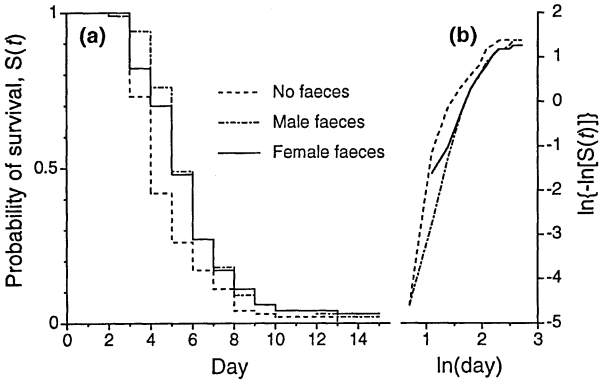

Fig. 3. Survival of second instars on adult male or female faeces. (a) Step plots show Kaplan–Meier estimates of the probability of a nymph surviving to any of the first 15 days after the first larval moult. (b) The complementary log plots were obtained by transforming the data in (a). Twenty newly ecdysed second instars were placed in Petri dishes containing water and either no faeces or adult male or female faeces, and mortality was recorded daily. The results of five replicates, 20 nymphs each, were pooled before calculation of Kaplan–Meier estimates.

Diet choice in different life stages

The adaptive benefit of ingesting faeces, coupled with the longer survival of nymphs on high-protein faeces, suggested that first instars might prefer a high level of protein in their diet. This hypothesis was tested by comparing the dietary preferences of neonates and adults. Newly eclosed adult males or females were simultaneously offered a high-protein (55% protein, 30% carbohydrate) and low-protein (5% protein, 70% carbohydrate) diet. Adults of both sexes ingested about four-fold more of the high-carbohydrate diet (Fig. 5), in contrast to neonates, which consumed the two diets in nearly a 1 : 1 ratio. The greater propensity of first-instar *B. germanica* to eat high-protein food and higher survivorship of starved nymphs on high-protein faeces suggest that growth and development of first instars are most efficient on such foods.

Discussion

Previous investigations on coprophagy in *B. germanica* focused on ways to exploit this behaviour in the transmission of insecticide from cockroaches that ingested it to those that did not (Silverman *et al*., 1991; Kopanic & Schal, 1997, 1999). What has remained unstudied, however, is whether cockroaches derive a measurable benefit from this behaviour. The survival of starved nymphs given either no faeces or adult male or female faeces was therefore compared in this study. This design is justified because the German cockroach, like other pests of human-built structures, tends to live in mixed aggregations composed of nymphs and adults. They presumably accrue some benefits from group living, such as an altered, favourable microclimate, alarm and antipredator tactics, and faster development and reproduction (Schal *et al*., 1997). Notwithstanding, trophic interactions such as the exchange of nutrients, symbiotic microbes, or both, probably

Table 3. Chemical compositions of the experimental diets and of the faeces of adult females fed these diets†.

	High protein	Medium protein	Low protein	Rat chow
Diets				
Lipids	7.5 ± 0.48	6.0 ± 0.68	6.5 ± 0.38	4.1 ± 0.11
Carbohydrates	33.4 ± 1.25	63.1 ± 0.67	76.1 ± 3.23	11.3 ± 0.13
Proteins	54.4 ± 3.06	23.0 ± 2.54	5.7 ± 0.60	23.2 ± 2.34
Nitrogen	7.9 ± 0.19	3.3 ± 0.09	0.5 ± 0.06	3.6 ± 0.03
Calories	4759 ± 30	4331 ± 23	4012 ± 9	4059 ± 14
Faeces				
Lipids	3.7 ± 0.68	5.4 ± 0.24	6.9 ± 1.11	3.0 ± 0.14
Carbohydrates	1.1 ± 0.14	2.8 ± 0.18	5.9 ± 0.11	2.2 ± 0.08
Proteins	17.6 ± 0.46	5.6 ± 0.12	3.1 ± 0.18	14.6 ± 0.26
Nitrogen	6.8 ± 0.22	2.3 ± 0.12	1.1 ± 0.03	3.6 ± 0.06
Calories	4113 ± 33	3815 ± 10	3531 ± 16	3571 ± 8

†Numbers represent the percentage by mass of diets and faeces composed of lipid, carbohydrate, protein, or nitrogen. Calories are per gram of diet or faeces. Means ± SEMs are the result of three measurements on separate samples, except for caloric determinations, which were based on two replicates. Faeces were from females fed either rat chow or one of three experimental diets (Table 1).

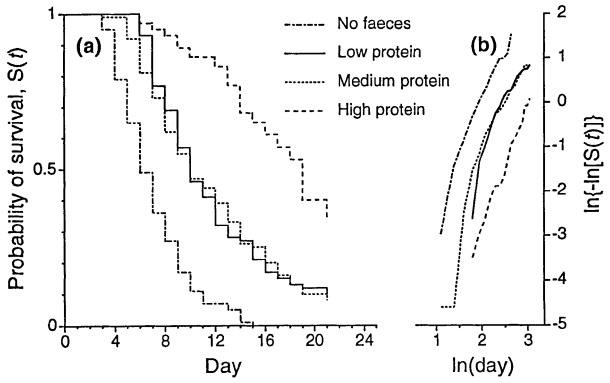

Fig. 4. Survival of first instars on the faeces of adults fed different diets. (a) Lines show Kaplan–Meier estimates of the probability of a nymph surviving to any of the first 21 days after hatch. The Kaplan–Meier estimates and ages were transformed to yield the complementary log plots in (b). The results of five replicates, 20 insects each, were pooled before calculation of Kaplan–Meier estimates.

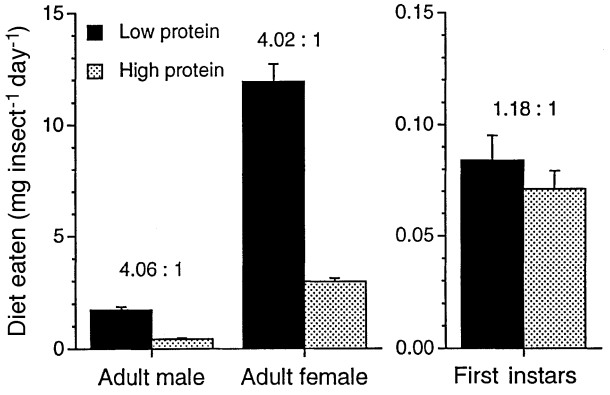

Fig. 5. Diet choice of adults and nymphs. Twenty adult males or females or 50 first instars were offered equal quantities of a high- (50%) and low- (5%) protein diet. Intake of each diet was measured gravimetrically every 24 h for 72 h. Bars represent the mean diet eaten per insect per day over the 3-day period. Error bars show + SEM. The ratio of low protein to high protein diet consumed is shown above each pair of bars. $N = 10$ for adult males and females and 12 for first instars.

play a pivotal role in the evolution and maintenance of such aggregations. Because young nymphs tend to be more sedentary than adults, it was hypothesised that coprophagy would serve neonates more than older nymphs.

The results of survival assays indicate that adult faeces can serve as an important nutritional buffer for first-instar *B. germanica*. Given no source of food other than conspecific faeces, neonate cockroaches died at about one-sixtieth the rate of first instars deprived of faeces (Table 2, Fig. 1a). Moreover, first instars given female faeces were more likely to moult into the second stadium than nymphs given male faeces, but more work is needed to determine whether this was due to quantitative or qualitative differences between male and female faeces. Significantly, however, neonates that hatched from field-collected females within 3 days of collection also survived significantly longer with adult faeces than without (Fig. 2), suggesting that coprophagy might impart a survival benefit to first instars in their natural setting.

In contrast to first instars, second instars provided adult faeces survived only slightly longer than starved counterparts. Second instars may have ingested only small amounts of faeces, derived only marginal benefits from their ingestion, or both. The results of previous investigations support the former hypothesis. Using faeces laced with a tracer dye, Kopanic and Schal (1999) demonstrated that second instars consumed less faecal material than did first instars. This was confirmed by an additional experiment in which the dye was replaced with a slow-acting insecticide, hydramethylnon. More than 90% of first instars fed insecticide-laden faeces died within 4 days, while less than 30% of second instars died within 4 days (Kopanic & Schal, 1997). Notably, second instars do survive longer (Fig. 3) on what little faeces they consume, although even a four-fold increase in the abundance of adult faeces failed to elevate their survival to the level of first instars. Faecal feeding therefore appears to be stage-specific, as is the benefit derived from it.

The adult diet influenced the nutritional quality of their faeces, which in turn affected nymphal survival. An early hypothesis stated that the low-protein (high carbohydrate) diet would yield *high-energy* faeces that would sustain starved nymphs for the longest time. Although these diets were relatively iso-caloric (Table 3), the combined sugar and lipid content of the faeces of females fed the low-protein diet was higher than that of the faeces of females fed the other diets (12.8 vs. 4.8 and 8.2%), suggesting that highly utilisable sources of energy might be more abundant in low-protein faeces. Yet, nymphs survived longest, and even grew, on the faeces of adults that were fed either rat chow (lowest lipids and carbohydrates; 14.6% faecal protein) (Fig. 1) or the high-protein artificial diet (low lipids and carbohydrates; 17.6% faecal protein) (Tables 2 and 3, Fig. 4). First-instar survival thus appears to be highest on faeces rich in protein (14.6 and 17.6%) and lowest on faeces with a lower protein content (3.1 and 5.6%). Interestingly, dietary protein levels > 5% are needed to support maximal rates of reproduction in adult female *B. germanica*, and dietary protein levels < 15% cause a reduction in juvenile hormone biosynthesis and a retardation of oocyte maturation (Schal *et al.*, 1993). Similarly, nymphal development is affected significantly by both the quality and quantity of protein in their diet (Cooper & Schal, 1992).

Presumably, both adults and nymphs engage in dietary *self-selection* or *diet mixing*, as do the brownbanded cockroach *Supella longipalpa* (Cohen *et al.*, 1987) and various phytophagous insects (Waldbauer & Friedman, 1991). If so, the diets (or faeces) that sustain development (or survival) better should be preferred in choice assays to diets or faeces that fail to do so. Compared with adults, first-instar *B. germanica* include a much higher fraction of high-protein food in their diet mixing (Fig. 5). It is not yet known, however, whether this diet mix

results in more efficient growth and development, and, given a choice, whether nymphs would prefer adult faeces containing high protein over low protein faeces. Clearly, though, an important relationship emerged between the quality of diet that nymphs ate *ad libitum* and the quality of the faeces that prolonged the survival of starved nymphs. Together, these data suggest that faecal protein may be an important factor influencing nymphal survival when other food sources are scarce.

It is possible, nevertheless, that neonates procure other faeces constituents that serve equally important roles in promoting their survival. For example, they might acquire adult-derived symbiotic microbes, however preliminary data fail to support this idea. Gut-defaunated first instars that hatched from metranidisole-treated females whose oothecae were detached and surface-sterilised developed normally (R. J. Kopanic, unpublished). Also, starved first instars survived equally on the faeces of metranidisole-treated adults and on the faeces of untreated adults; yet both sets of faeces enhanced survivorship significantly. It thus appears that faecal nutrients, especially faecal protein, serve as primary trophic factors that promote neonate survival.

Coprophagy may represent the ancestral condition of proctodeal feeding, which is common in termites and subsocial cockroaches. Ovoviviparity probably promoted the evolution of gregariousness and coprophagy in non-social cockroaches. The neonates of all cockroaches are at least transitionally gregarious because cockroach eggs are aggregated within oothecae (Roth, 1970); the young nymphs either remain clustered or disperse to live solitarily. In ovoviviparous cockroaches, including *B. germanica*, however, unlike oviparous cockroaches (e.g. *Periplaneta americana*), the female carries the brood for the duration of its embryonic development. The female gives birth to neonates, which places the progeny in close proximity to adults. The patchy distribution of suitable microhabitats and relatively low mobility of nymphs probably promoted the evolution of gregariousness and chemical signalling associated with it. Coprophagy could then have evolved as a mechanism for the young and relatively sedentary aggregated nymphs to utilise local resources maximally and minimise foraging forays.

Central to the evolution and persistence of coprophagy is *B. germanica*'s dependence on food for development and reproduction (Kunkel, 1966; Schal *et al*., 1993, 1997). In each stadium, nymphs feed intensively before committing to the next moult. Nymphs also accumulate nutrient reserves that can be utilised when food is scarce, thereby permitting survival during periods of nutrient deprivation. For example, the German cockroach, like other cockroaches, can sequester nitrogen in urates when it eats food rich in protein. Nitrogen can be mobilised from the urates when it becomes limiting in the diet (Cochran, 1985). Neonates must procure food, but they are nutritionally unique in that their preceding developmental stage is the embryo, which has received all its nutrients, primarily in the form of vitellin (Raikhel & Dhadialla, 1992), from the mother during oogenesis. In some insects, for instance firebrats (Watson, 1967), the oocytes are provisioned by the mother with sufficient nutriment to sustain its progeny through one or more post-embryonic moults. Newly hatched nymphs of the German cockroach must, however, feed to develop. Given the small size of neonates, and their concomitant limited foraging capability, it appears that an adaptive benefit of coprophagy would be to augment nutrient procurement while allowing first instars to remain in a fixed, and perhaps safe, location. First instars are far less likely than older nymphs to forage long distances from a shelter (Cloarec & Rivault, 1991; Kopanic & Schal, 1999). Whether a first instar will forage depends greatly on its proximity to a food resource, and the level of coprophagy by first instars in both laboratory and field assays nearly doubles as the distance between a first instar's shelter and food increases from 5 to $\geqslant 1120$ cm (Kopanic & Schal, 1999). Food resources are highly patchy and unpredictable in structural habitats, suggesting that neonates would probably engage in starvation-induced coprophagy in nature.

Several issues regarding coprophagy in the German cockroach remain to be addressed. The differences in coprophagous behaviour between first and second instars may be related to first instars being endowed with maternally derived micronutrients, which have carried over from the embryonic stage. This might, in some way, foster neonatal consumption of nutritionally incomplete material, such as faeces. It is important to note that nymphs in the current study were provided with no food source other than faeces. The faecal exchange of symbiotic organisms also needs to be studied. Addressing all these issues would result in a much improved understanding of the nutritional ecology of *B. germanica*, a subject of great contemporary interest because of the current emphasis on baiting tactics in cockroach control programmes.

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