Effect of Diet Quality on Survival and Reproduction of Adult *Paederus fuscipes* (Coleoptera: Staphylinidae)

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ABSTRACT The survival and reproduction of the beetle *Paederus fuscipes* Curtis on diets that differed in macronutrient composition were investigated in the laboratory. The sex organs of females fed each test diet were dissected to evaluate the ovarian development over time. Adults fed on a carbohydrate-rich diet lived longer than adults fed the other diets, but this diet provided insufficient nutrients for reproduction. Females fed on a protein-rich diet had high fecundity; however, the mean longevity of reproductive adult *P. fuscipes* significantly was shortened by 20–30 d compared with longevity of 60–70 d for adults fed a carbohydrate-rich diet. In contrast, adults that were provided lipid-rich diet had low survival and fecundity. Overall, the development of previtellogenic follicles was significantly affected by diet regime and days since starting a particular diet. The follicle size of females given protein-rich diet increased 0.5-fold 2 wk after beginning the diet. In contrast, the development of the follicles was slow in females given the carbohydrate-rich diet and the follicles degenerated in females given the lipid-rich diet. In terms of ovarian maturation, females fed on a protein-rich diet contained mostly vitellogenic and chorionated follicles. In contrast, the ovarioles of females on the carbohydrate-rich diet were largely occupied with previtellogenic and vitellogenic follicles, whereas for a lipid-rich diet, the follicles remained at the previtellogenic stage throughout the experiment.

KEY WORDS rove beetle, *Paederus dermatitis*, reproduction development, vitellogenesis, predator

Food quality greatly influences life history traits such as survival, development, and fecundity of an insect in nature (Dittman and Biczkowski 1995, Wheeler 1996, Davey 1997, Joern and Behmer 1997, Adams 1999). In general, carbohydrate is the main energy source to support optimum growth, development, and survival of most insects. However, a carbohydrate-rich diet modulates insect metabolic rate by decreasing the energy expenditure on reproduction (Naya et al. 2007). The energy obtained from a carbohydrate-rich diet is mainly focused on insect's life maintenance, thus prolonging the life span in insects (Lardies et al. 2004). In other words, carbohydrate plays only a small to no role in life history trade-offs in arthropods (Zera and Larsen 2001). However, protein is often regarded as an important nutritional element for insect reproduction, particularly in contributing to higher rates of production of offspring by females (Joern and Behmer 1997, Aron et al. 2001, Romeis and Wäckers 2002, Wall et al. 2002, Lardies et al. 2004). However, this causes a significant life history trade-off in females (Lardies et al. 2004). Several reports indicated that an adequate amount of lipid in the diet is beneficial to insect reproduction (Naya et al. 2007) and survival (Ujvari et al. 2009), as well as providing a main energy source for flying insects (Zera et al. 1999). It provides twice the amount of energy compared with protein and carbohydrate (Ujvari et al. 2009). Apart from that, a lipid-rich diet helps to boost the insect tolerance to desiccation (Hadley 1980, Howard and Blomquist 2005). However, high lipid intake has a detrimental impact on insects, for instance, shortening life span and decreasing egg production (Ujvari et al. 2009).

Arthropod predators often require high protein intake for reproduction to maintain population size (Denno and Fagan 2003, Matsumura et al. 2004). For example, Jensen et al. (2012) found that the predatory beetle *Anchomenus dorsalis* (Pontoppidan) often forages for protein-rich prey or consumes low-quality prey more than needed for optimal reproduction. In a previous study, we established the life table of *Paederus fuscipes* Curtis (Coleoptera: Staphylinidae) under ideal controlled laboratory conditions. Adult *P. fuscipes* lived for 42–58 d and the females laid substantial numbers of eggs (i.e., 121–147 eggs laid per female) when fed on the lobster cockroach [*Nauphoeta cinerea* (Olivier)]. The females were even capable of increasing the reproductive output when mortality risks rose so as to sustain the progeny in the population (Bong et al. 2012). This species encounters abundant prey under natural conditions. The nutritional values of its phytophagous prey, particularly orthopterans, vary depending on species from 13.7 to 64.2% crude protein (Bukkens 1997). However, most prey species are protein-poor owing to their nutrient-

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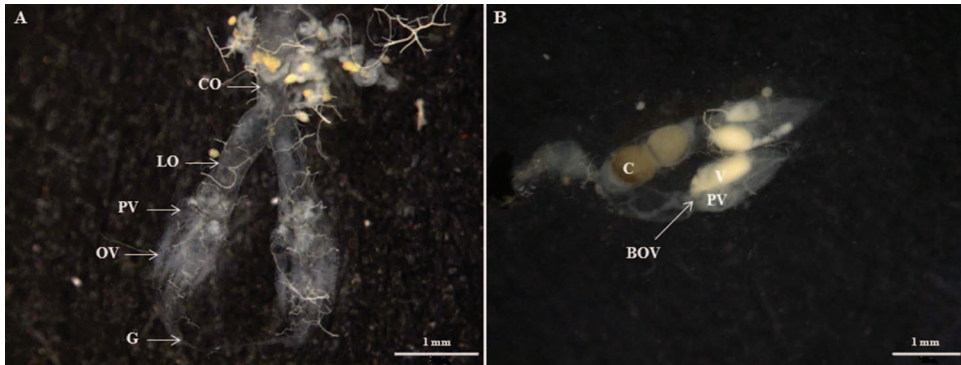[3] Corresponding author, e-mail: zairi@usm.my.

Fig. 1. Ovary of female *P. fuscipes* from (A) 0-d female, and (B) 21-d unmated female feeding on cockroach. CO, common oviduct; LO, lateral oviduct; BOV, base of ovariole; OV, ovariole; G, germarium; PV, previtellogenic follicle; V, vitellogenic follicle; C, chorionated follicle. (Online figure in color.)

poor plant diets. According to Mayntz and Toft (2001), the type of diet consumed by prey determines nutritional quality of food for arthropod predators. Food quality affects reproductive performance of predators. Thus, the quality of available prey in the field is likely the key factor influencing the life history strategies of *P. fuscipes.* This article is the continuation of a previous study (Bong et al. 2012) and investigates the effects of diet quality on survival and reproductive output of *P. fuscipes.*

We predicted that *P. fuscipes* would adopt different life trait strategies in response to environmental circumstances, at least, in rice fields where the prey population is fluctuating in response to the annual cropping cycle and climatic variation (Win et al. 2011). To better understand the impact of diet on the life history of *P. fuscipes*, we first investigated the survival and reproductive capability of individuals fed protein-rich, carbohydrate-rich, and lipid-rich diets. The sex organs of females kept on each of the experimental diets were dissected to evaluate ovarian development over time until the females were fully mature for oviposition.

Materials and Methods

Insect Sampling. Adult *P. fuscipes* were collected from an infested high-rise building in mainland Penang, Malaysia: Desa Wawasan (5° 21′21.38″ N, 100° 26′50.82″ E, 9 m elevation). The building is located ≈1.89 km from the Permatang Pauh rice fields from where the *P. fuscipes* had dispersed.

Rearing Method. The adult beetles were reared in an insectarium of the Vector Control Research Unit, School of Biological Sciences, Universiti Sains Malaysia, at 28.0 ± 0.2°C, 63.5 ± 2.0% relative humidity (RH), and a photoperiod of 12:12 (L:D) h. The rearing method was adopted from Bong et al. (2012).

Diets. Three types of foods varying in carbohydrate, protein, and lipid content were tested. Late nymphs of the lobster cockroach (CK) were provided herein as protein-rich food (63.7% protein, 26.5% lipid, and 6.5% carbohydrate [Koay 2005]). The late nymphs were

killed by freezing. Dry dog food (DF; Purina, Rayong, Thailand) was a carbohydrate-rich food (8.0% protein, 10.0% lipid, and 50% carbohydrate), and smashed-hard-boiled egg yolk (EY) was a lipid-rich food (28.2% protein, 62.6% lipid, and 3.7% carbohydrate [Eow 2004]). The diets were stored frozen before feeding.

Survival and Fecundity of *P. fuscipes*. First filial generations of newly emerged adult males and females were sexed and paired. Each pair was kept in a plastic container (2.5 cm in diameter by 1.5 cm in height) that was layered with a moist filter paper. Each day, the pairs were provided with ≈0.2 g of the aforementioned diets, and moist cotton as water supply and oviposition site. The adult survival rate and eggs laid were counted daily. If the male of a pair died, it was replaced with another one to ensure oviposition was resumed.

Ovarian Development. The field-collected females of *P. fuscipes* were divided into five treatments: 1) CK-fed mated female, 2) CK-fed unmated female, 3) DF-fed mated female, 4) DF-fed unmated female, and 5) EY-fed unmated female. The EY-fed mated female treatment was not attempted because cannibalism occurred when EY was given to the pairs (see Results). However, by no choice of other foods, a single female was confined with only the EY as lipid-rich diet to ensure the diet was consumed to assess the effect of lipid-rich diet on ovarian development. For mated female treatments, a female *P. fuscipes* was paired with a male throughout the experiment before observation, while unmated females were reared individually. For controls, females were also reared individually and provided only moist cotton buds for water but without food. They were dissected after 14 d. Ovarian development ($n = 15$) was assessed for each treatment at day 0 (soon after collection from the field), 5, 14, and 21.

An incision was made laterally between the dorsal tergites and ventral sternites from the thorax to the tip of abdomen. The entire tergites, sternites, as well as adipose tissues attached to the ovaries were removed carefully. The pair of ovaries (Fig. 1A) was placed on a microscope slide in a drop of saline and examined

Table 1. Adult longevity and reproduction of *P. fuscipes* feeding on different diets

Diet	DF		CK		EY	
	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE
Adult longevity (d)						
Female	26	74.1 ± 6.7a	40	42.3 ± 3.8b	35	15.4 ± 2.2c
Male	27	64.1 ± 8.6a	49	43.3 ± 4.0b	50	12.7 ± 2.0c
Reproduction						
*Lifetime fecundity per female (eggs)	26	2.6 ± 1.3a	40	121.3 ± 16.0b	35	0 ± 0
*APOP (d)	7	38.4 ± 8.1a	33	20.3 ± 2.3b	NA	NA

DF, dog food; CK, cockroach; EY, egg yolk; APOP, adult preoviposition period; NA, not available.

Mean values followed by the same letter in the same row are not significantly different (Tukey's HSD; $P > 0.05$, *Student's t-test; $P > 0.05$).

with a dissecting microscope at 10–40× magnification. The six ovarioles in an ovary were not teased apart to avoid damage. All follicles (Fig. 1B) within the ovarioles were measured at the greatest width and length and scored as follows: 0, no follicle formation; 1, developing follicle at previtellogenic stage; 5, vitellogenic follicles with yellowish yolk granules; and 10, mature chorionated follicle (Adams 2000). The scores from all ovarioles were summed as a total ovarian score.

Statistical Analysis. Before the statistical analysis, all data were checked for normality using the Kolmogorov–Smirnov test. When a criterion of normality was not met, a Log_{10} transformation was performed. The
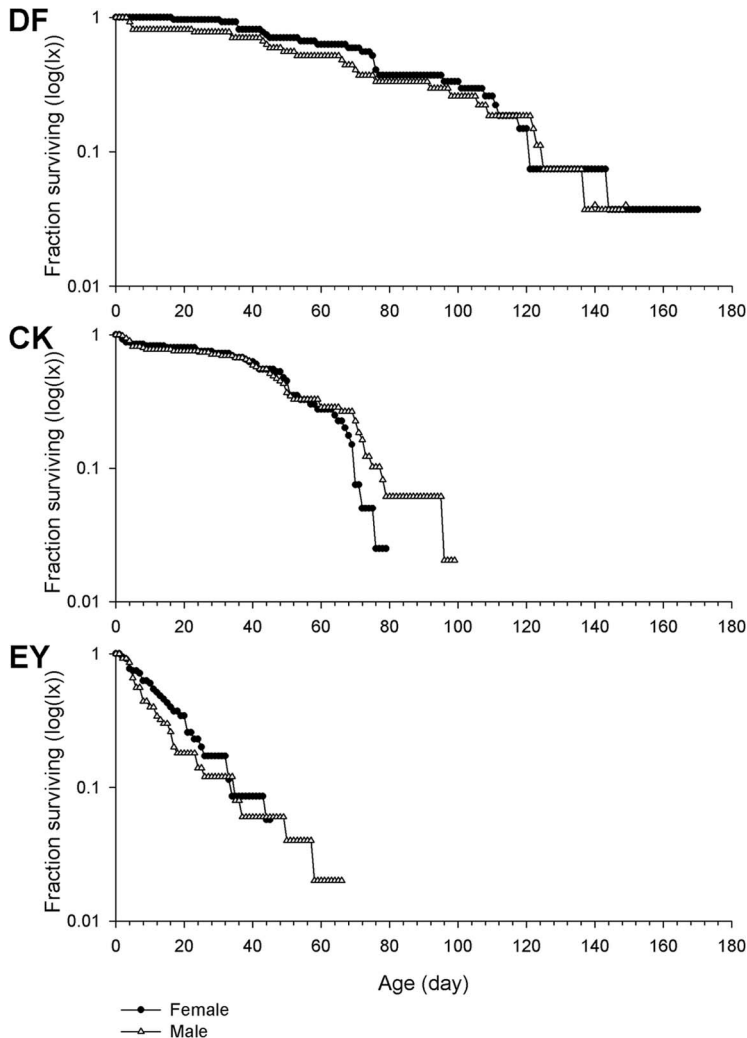
Fig. 2. Survival of *P. fuscipes* feeding on three different diets. DF, dog food; CK, cockroach; EY, egg yolk.
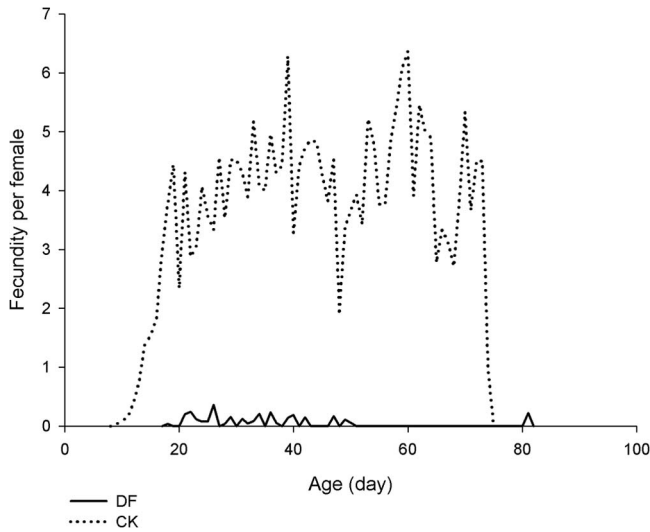
Fig. 3.   Egg production of *P. fuscipes* feeding on different diets. DF, dog food; CK, cockroach.

interaction between gender and diets on adult longevity, and the effects of diet on the size of previtellogenic follicles at the selected times were examined using the two-way analysis of variance (ANOVA), and means were separated by Tukey's honestly significant difference (HSD) test. The egg production of females feeding on CK and DF was compared using an independent Student's *t*-test. Total number of follicles of mated and unmated females feeding on test diets at the selected days was examined with ANOVA using the General Linear Models (GLM) Procedure, and means were separated using Tukey's HSD test, while ovarian score was tested using the Scheirer–Ray–Hare test, an extension of the Kruskal–Wallis test. All analyses were performed using SPSS analysis version 11.0 (SPSS Inc., Chicago, IL) at $\alpha = 0.05$.

Results

Survival and Fecundity. Diet significantly affected the longevity of adult *P. fuscipes* ($F = 43.581$; df = 2, 216; $P < 0.001$). However, there was no significant interaction between gender and diet on longevity ($F = 1.885$; df = 2, 216; $P = 0.154$). The mean longevity of DF-fed adults was significantly longer compared with CK-fed and EY-fed adults (Table 1). Both the

DF-fed and CK-fed adults showed type I survivorship curves, which reflected low mortality during early age, with most individuals surviving to old age (Fig. 2). The survival rate of DF-fed and CK-fed adults decreased drastically at approximately day 100 and day 50, respectively. The survival rate of EY-fed adults decreased constantly over time partly owing to cannibalism (Fig. 2).

Overall, CK diet promoted oviposition in 83% of females compared with 26.9% of females fed on the DF diet. No oviposition was observed in EY-fed females (Table 1). CK-fed females laid an average of five eggs per day (Fig. 3). In contrast, females given DF produced nearly 60-fold fewer eggs throughout their lifetime ($t = -6.090$; $n = 38$; $P < 0.001$). Further, the preoviposition period of CK-fed females was significantly shorter than for DF-fed females ($t = 3.087$; $n = 38$; $P = 0.004$).

Ovarian Development. Mating status did not significantly affect the ovarian development of female *P. fuscipes* (Table 2). Therefore, the data of mated and unmated females were pooled. In general, both vitellogenic and chorionated follicles were formed 14 d after females were given CK and DF (Table 3). Vitellogenic follicles were oval in shape with a length of 0.75 ± 0.02 mm and a width of 0.37 ± 0.01 mm, while

Table 2.   Analysis of variance results for ovarian development of *P. fuscipes*

Source	Ovarian score				Total no. of follicles			
	Type III sum of square	df	Mean square	F	Type III sum of square	df	Mean square	F
Mating status	0.021	1	0.021	0.179	0.015	1	0.015	0.159
Diet	1.089	2	0.545	4.563[*]	0.538	2	0.269	2.925
Day	4.394	4	1.098	9.204[*]	3.444	4	0.861	9.372[**]
Mating status × diet	0.001	1	0.001	0.006	0.013	1	0.013	0.138
Mating status × day	0.113	4	0.028	0.236	0.059	4	0.015	0.161
Diet × day	1.855	8	0.232	1.943	1.004	8	0.125	1.365
Mating status × diet × day	0.281	4	0.070	0.589	0.026	4	0.006	0.069

*$P < 0.05$, **$P < 0.001$ (the P value of ovarian score were corrected using nonparametric Scheirer–Ray–Hare test).

Table 3. Mean number of follicles (± SE) over time in female *P. fuscipes* feeding on different diets

Day	CK				DF				EY			
	TF	PV	V	C	TF	PV	V	C	TF	PV	V	C
0	3.3 ± 0.9	3.3 ± 0.9	0	0	3.3 ± 0.9	3.3 ± 0.9	0	0	3.3 ± 0.9	3.3 ± 0.9	0	0
5	2.8 ± 0.4	2.8 ± 0.4	0	0	2.2 ± 0.2	2.2 ± 0.2	0	0	2.7 ± 0.5	2.7 ± 0.5	0	0
14	4.0 ± 0.4	3.3 ± 0.4	0.3 ± 0.2	0.2 ± 0.1	3.4 ± 0.4	2.9 ± 0.2	0.2 ± 0.1	<0.1	2.6 ± 1.0	2.6 ± 1.0	0	0
21	6.5 ± 0.6	5.0 ± 0.4	0.8 ± 0.3	0.4 ± 0.2	4.6 ± 0.4	4.2 ± 0.3	0.3 ± 0.3	<0.1	2.0 ± 0.6	2.0 ± 0.6	0	0

DF, dog food; CK, cockroach; EY, egg yolk; TF, total follicle; PV, previtellogenic follicle; V, vitellogenic follicle; C, chorionated follicle.

chorionated follicles were spherical with a diameter of 0.64 ± 0.01 mm.

No mature follicles were present in females dissected soon after they were collected from the infested building (0 d). This allows a more meaningful comparison regarding the effect of food on ovarian development. A possible bias in the experiment using field-collected females can now also be ruled out. The size of previtellogenic follicles was significantly affected by diet ($F = 29.074$; df = 2, 114; $P < 0.001$) and duration of diet given ($F = 20.118$; df = 4, 114; $P < 0.001$). In addition, the developmental rate of the previtellogenic follicles significantly depended on the types of food given ($F = 6.730$; df = 8, 114; $P < 0.001$). Particularly, the follicle size in CK-fed females increased 0.5-fold between day 0 to day 14 (Fig. 4). In contrast, the development of the follicles in DF-fed females was comparatively slow, with the follicle size on day 14 and 21 almost comparable with that at day 0. The size of previtellogenic follicles of EY-fed beetles decreased over time and was comparable with that of starved females, indicating that the development of those follicles was retarded and follicles were degenerating.

The total number of follicles of CK-fed and DF-fed females increased significantly over time and reached a total of five to six follicles per female on day 21 (Table 2 and Fig. 5). However, their maturation apparently differed between diets. As illustrated in Fig. 5, CK-fed females possessed a higher ovarian score than DF-fed females ($F = 4.563$; df = 2, 279; $P = 0.024$). Generally, by 21 d, most of the follicles found in the ovarioles of CK-fed females developed into vitellogenic and chorionated follicles. In contrast, the follicle maturation in DF-fed females was slow. By 21 d, most of the follicles were in previtellogenic stage, and only some have developed into vitellogenic follicles. The follicles in females feeding on EY remained at the previtellogenic stage throughout the experiment.

Discussion

The current study showed that diet quality greatly influenced survival and reproductive output in *P. fuscipes*. Of the three diets tested, adults feeding on the carbohydrate-rich DF had the longest life span. However, the diet did not provide sufficient nutrients for reproduction. Harvestman *Pachylus paessleri* Roewer had a low standard metabolic rate when given a carbohydrate-rich diet compared with a protein-rich diet (Naya et al. 2007). The general strategy of the insects is to channel acquired energy mainly into life maintenance rather than high cost events such as growth and reproduction in females. This allows insects to
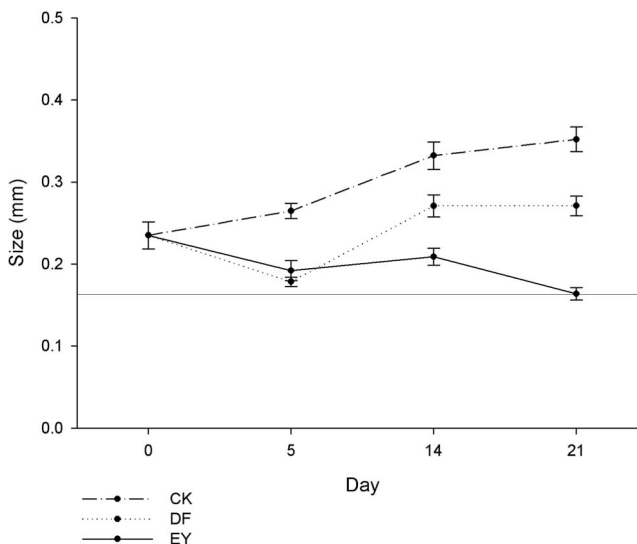
Fig. 4. Development of previtellogenic follicles of *P. fuscipes* feeding on different diets over time. Horizontal solid line represents the follicle size (0.1629 mm) of starved female at day 14. DF, dog food; CK, cockroach; EY, egg yolk.
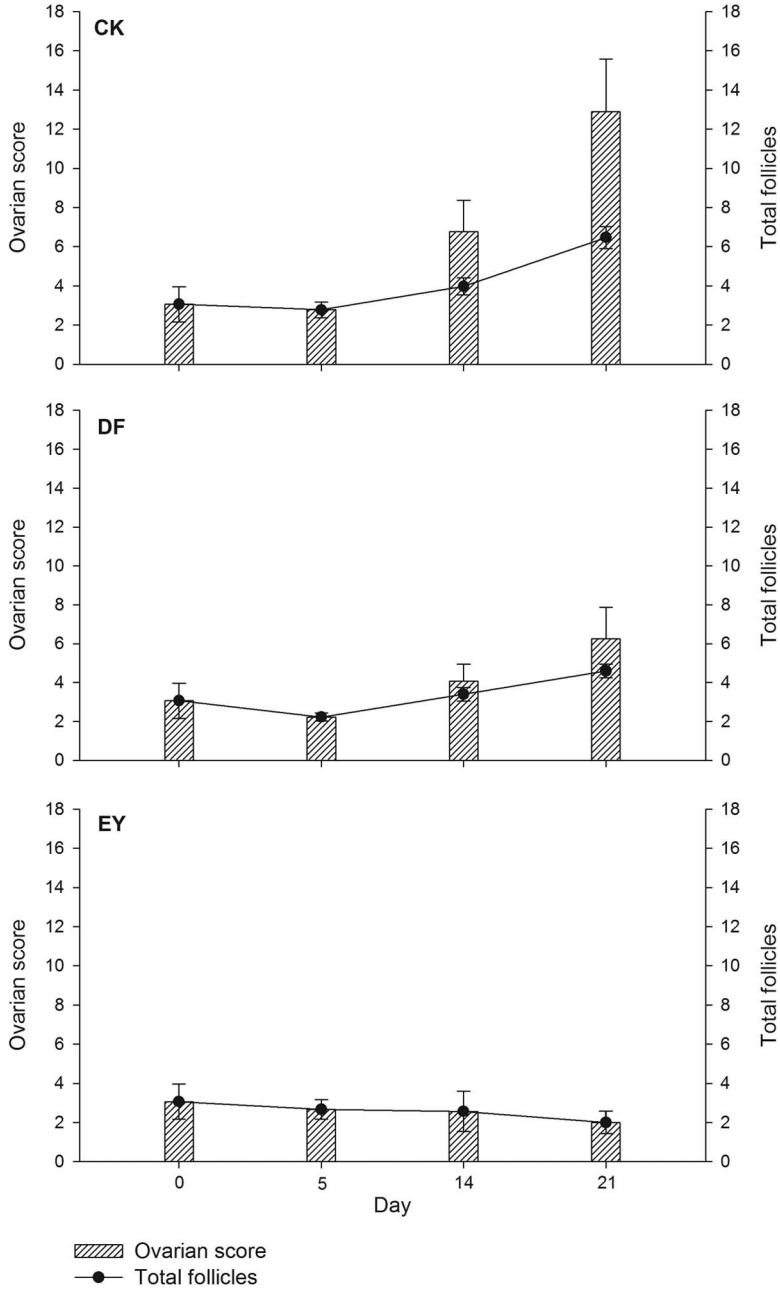
Fig. 5. Ovarian score and total follicles of female *P. fuscipes* feeding on three different diets over time. DF, dog food; CK, cockroach; EY, egg yolk.

survive while feeding on a low-quality diet. The results of our study are consistent with previous studies. For instance, grasshoppers, *Ageneotettix deorum* (Scudder), fed on diet containing 26.7% carbohydrate survived for 50.2 d, but only survived for 28.5 d when fed on diet containing 4.3% carbohydrate (Joern and Behmer 1997). Similarly, survival of a wolf spider, *Pardosa amenlata* (Clerk), given dog food-fed flies was significantly improved compared with those merely fed on protein, lipid, and vitamin diets (Joern and Behmer 1997, Mayntz and Toft 2001).

Adult females of *P. fuscipes* feeding on protein-rich CK laid substantially more eggs throughout their lifetime compared with DF-fed females. Reproduction of *Musca domestica* L. and *Drosophila melanogaster* Meigen was impeded when given carbohydrate without protein, but this was reversed when protein was provided (Bownes and Reid 1990, Adams and Gerst 1992,

Wheeler 1996). Likewise, the increases in reproductive rate were also recorded in a grasshopper following higher protein intake. For instance, the egg productivity of females given 4% of protein in the diet was 1.46 times greater than when given only 1% of protein (Joern and Behmer 1997). Insect reproductive output is quite responsive to changes in protein content in the diet (Smith and Northcott 1951, McCaffery 1975). Similar to the current study, 83% of females in the harvestman subjected to protein-rich intake oviposited, while only 20% of females on carbohydrate-rich diet oviposited, though clutch mass and egg number produced showed insignificant differences between the two diets (Naya et al. 2007).

However, reproduction comes at a fitness cost. The mean longevity of adult *P. fuscipes* given a protein-rich diet significantly shortened by 20–30 d compared with adults fed carbohydrate-rich diet, which lived for 60–70 d. As shown in a study of harvestman, the standard metabolic rate increased concomitantly with the number of eggs laid (Naya et al. 2007), indicating that reproduction required higher energy investment.

The present observation on follicle development also pointed to the importance of protein intake for reproduction (see Figs. 4 and 5 for the effect of diets on follicle size and ovarian score). In *M. domestica* and *D. melanogaster*, follicle development stopped at the previtellogenic stage when flies were given a carbohydrate-rich diet (Bownes and Reid 1990, Adams and Gerst 1992, Wheeler 1996). However, the current study showed that oogenesis of *P. fuscipes* was not affected by adult food, given that the increment of the number of follicles over time between carbohydrate-rich and protein-rich diets was insignificant (see Fig. 5). This was in accordance with Wittmeyer et al. (2001) who noted that oogenesis in *Podisus maculiventris* (Say) fed live *Trichoplusia ni* Hübner larvae showed no significant difference compared with individuals fed artificial diet, but vitellogenesis in females kept on artificial diet was retarded. This indicated that adult food played a major role for follicle maturation. However, diet might not be the sole factor in enhancing reproductive output of a female *P. fuscipes*. The observation of high egg loads (chorionated follicles) in unmated females fed protein-rich diet may indicate mating as the underlying stimulus mechanism. This phenomenon is evident in unmated female of *P. maculiventris* (DeClercq and Degheele 1997) and *Rhodnius prolixus* Stål (Davey 1967, Wang and Davey 1993). Males trigger physiological effects with the sperm as well as nutritional transfers (Butlin et al. 1987, Boggs 1990, Wheeler 1996). The closely related rove beetle, *Aleochara curtula* Goeze, mated every 24–32 h to ensure maximal fecundity and fertility throughout its lifetime (Gack and Peschke 1994).

An adequate intake of lipid diet was reported to be of prime importance for the reproduction of female arthropod predators (Mayntz et al. 2005, Jensen et al. 2012). The carabid beetle, *A. dorsalis*, exhibited maximum fecundity when given a diet of lipid and protein (L:P) in the proportion of close to 0.5 (Jensen et al. 2012). These results accord with our observation

when *P. fuscipes* is given a protein-rich diet with a similar ratio of L:P. However, high concentrations of lipid in the *P. fuscipes* diet might have detrimental effects for both survival and reproduction. Adults feeding on a diet high in lipids lived on average only up to 2 wk, and the ovarian development was retarded and follicles were degenerating (oosorption). Similarly, longevity decreased significantly to 20–30 d in *Calliphora stygia* (F.) adults feeding on lipid-rich food. They also failed to reproduce when given high concentrations of lipid in the diet (Ujvari et al. 2009). However, our findings should be viewed with caution because the amount of food consumption was not determined in this study. The degenerating follicles might also be owing to starvation.

The current findings have offered some important insights into the life history traits of *P. fuscipes* associated with prey availability in nature. For instance, *P. fuscipes* encounter abundant phytophagous prey (Manley 1977) that has low protein content owing to their nutrient-poor plant diet. This poses dietary constraints on *P. fuscipes*, and consequently, it might selectively forage for particular prey with adequate proportions of nutrients (L:P) for its reproduction, similarly to predatory ground beetles (Mayntz et al. 2005, Jensen et al. 2012). Alternatively, *P. fuscipes* may overconsume low-quality prey to meet its nutritional needs (Stephens and Krebs 1986). Otherwise, reproduction could not occur and all acquired energy is mainly to prolong their life span. This scenario might occur particularly when the prey population is drastically reduced following the rice crop harvest.

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