RESEARCH ARTICLE

Study of inheritance of feeding potential in natural populations of predatory coccinellid *Cryptolaemus montrouzieri* Mulsant using isofemale strains

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Abstract

The ability to feed on the prey is of great concern for the predatory insects, especially with regard to predatory coccinellid, *Cryptolaemus montrouzieri* Mulsant, which is mass reared and released into the field in large numbers to control the target pests. The variability associated with feeding potential is partly influenced by the genetic background of the insects and partly due to the environment, but the genetic basis of this trait is not yet fully understood in *C. montrouzieri*. The aim of this study was to identify the genetic basis of variation and heritability of this quantitative trait in natural populations of *C. montrouzieri* through isofemale heritability and parent–offspring regression. The regression analyses indicated that there was a significant linear relationship between progeny and their mothers for feeding potential.

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Introduction

Feeding potential is the maximum number of prey a predator can consume in a unit time. This is an important trait for predatory insects that are used in integrated pest management programmes. The Australian ladybird beetle, *Cryptolaemus montrouzieri* Mulsant (Coleoptera: Coccinellidae) is a potential predator on several homopteran insects like mealy bugs, scales, aphids, mites and white flies (Sullivan *et al.* 1991; Drea and Gordon 1990; Frazer 1988; Chanzeau 1985; Mani and Krishnamoorthy 1990). In particular, *C. montrouzieri* is considered very effective predator against mealy bugs as both grubs and adults feed on all stages of mealy bugs. However, the adults of *C. montrouzieri* are considered as the most efficient predatory stage compared to grubs (Rosas-Garcia *et al*. 2009; Ghafoor *et al*. 2011). The coccinellid, *C. montrouzieri* has been introduced into several countries for biological control programmes with varied success (Dixon 2000). The discrepancies in the feeding potential of this predator noticed by earlier workers might be attributed to the variations in the stage of the prey, prey density and environmental conditions.

Several studies have explained the feeding potential of predatory coccinellid *C. montrouzieri* under different situations (Srinivasan and Babo 1989; Mani *et al*. 1990; Mani 1998; Mangoud 2006; Amal *et al*. 2010). Despite the importance of *C. montrouzieri* as major biocontrol agent, understanding the genetic basis and degree of inheritance of feeding potential in *C. montrouzieri* is poor.

The intraspecific variation in the behavioural responses of predators constitute a central but relatively neglected feature in the predator–prey associations (Arnold 1986, 1992; Krebs and Kacelnik 1991; Catherine *et al*. 1995). Traits related to behaviour, morphology, physiology (Fuiman and Cowan 2003) have a genetic basis (Conover and Munch 2002; Sanford *et al*. 2003) and can be learned (Dukas and Bernays 2000). Behavioural traits including feeding are inherently flexible (Blanckenhron and Perner 1994), often due to other factors like learning and immediate environmental conditions. Current theory suggests that most phenotypic expressions of behavioural traits result from a complex interaction between genes and environments (Barlow 1991). Recent studies of genetic variation of morphological traits, namely wing length, thorax length, wing traits and bristle number in *D. melanogaster* reported varied genetic variances/heritabilities in extreme environments (De Moed *et al*. 1997; Hoffmann and Parsons 1988; Hoffmann and Schiffer 1998;

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Woods *et al*. 1999; Imasheva *et al*. 1999; Bubliy *et al*. 2000). Studies in other insects have clearly established the genetic and environmental influences on intraspecific feeding differences (Kause *et al*. 1999).

Our attempts to study the genetic variability in the feeding potential of *C. montrouzieri* met with obstacles as the laboratory maintained populations lost variability in their feeding after two to three generations. Therefore, we resorted to evaluate genetic variability of feeding potential in natural populations of *C. montrouzieri* through isofemale strains that provide a relatively simple though crude approach to the assessment of polygenic variation in natural populations (Hoffmann and Parsons 1988; David *et al*. 2005). Responses to selection are partly determined by additive genetic variation (Bubliy *et al*. 2001), and the magnitude of genetic influence on behavioural traits can be determined through heritability estimates (Megan *et al*. 2005). Isofemale strains have been used to examining genetic variation in ecological and behavioural traits in insects like *Priophorus pallipes* for final larval mass and development time (Kause and Morin 2001); *Nicrophorus pustulatus* for body mass at hatching and development time (Rauter and Moore 2002); *Stator imbatus* for egg length, lifetime fecundity (Czesak and Fox 2003) and *Pholcus phalangioides* for body size, development time and body mass (Uhl *et al*. 2004). In spite of many limitations, the isofemale line technique (ILT) remains a popular method for characterizing quantitative traits in natural populations (David *et al*. 2005). The present study documents the nature and range of phenotypic variation in the feeding potential of predatory coccinellid, *C. montrouzieri* with underlying genetic influence through isofemale lines. Usually, isofemale strains can provide very crude initial heritability estimates if strains are tested soon after their establishment in laboratory when maintained at a fairly large population size. In the present study, the feeding potential was measured on the first laboratory generation among individuals which are full-sibs, but noninbred. To estimate the relationship between the amount of variation determined by genetic as well as non-genetic factors, the coefficients of genetic variation (CV_G) and residual variation (CV_R) were calculated as described by Kause *et al*. (2001).

Materials and methods

The study was conducted at the Indian Institute of Horticultural Research, Bangalore, in southern India (12°58′N; 77°35′E). The *C. montrouzieri* isofemale mothers used in the experiment were collected from wild cotton (*Gossypium hirsutum*) heavily infested with the pink hibiscus mealy bug, *Maconellicoccus hirsutus* Green (Homoptera: Pseudococcidae) in Bangalore during July and August 2009. These field-caught isofemale mothers were collected in individual vials and immediately shifted to the laboratory. A total of 20 wild-mated ovipositing female *C. montrouzieri* were used to find isofemale lines for the experiment. Under laboratory conditions, *M. hirsutus* reared on pumpkin (*Cucurbita moschata*) was used for feeding the grubs and adults of *C. montrouzieri* (Kairo *et al*. 1997). Each isofemale mother was placed in an independent 9-cm diameter Petri dish (∼64 cm^2) lined with Whatman filter paper (90-mm diameter) and provided with 10 s instar mealy bugs, *M. hirsutus* per day. Observations on number of mealy bugs consumed per day were made continuously for 15 days. The eggs from each individual isofemale mothers were collected as and when they laid and maintained separately in Petri dishes to find the first laboratory generation. From each mother about 50 eggs were collected randomly and each of the egg was kept separately in a Petri dish at 23 ± 2°C, LD 12:12 h and reared till pupation. After adult eclosion from each isofemale group, 30 adult beetles were selected randomly irrespective of size and sex to find respective isofemale families. The 30 adult beetles from each isofemale family were assessed for their feeding potential continuously for 15 days by providing fixed number of second instar mealy bugs *M. hirsutus* (10 per day) in individual Petri plates and observations were made on number of mealy bugs consumed by each beetle.

The feeding data of isofemale mothers and their respective families (30 individuals per family) were used for further analysis. The statistical analyses were carried out on untransformed data using procedures described by Zar (1996) as transformation can obscure the inherent trend in the data. The feeding potential was compared across lines using analysis of variances and intraclass correlations (Hoffmann and Parsons 1988; Falconer 1989). The genetic variability was estimated by the coefficient of intraclass correlation, *t*. These estimates include genetic effects in their broadest sense, encompassing dominance and epistasis as well as additive effects. In quantitative genetics, heritability (h^2) estimates the amount of additive genetic variability which is transmitted from the parents to offspring (David *et al*. 2005), h^2 was calculated from '*t*' as given by Falconer (1989). The genetic and residual coefficients of variations were calculated as per Kause *et al*. (1999). In all analyses, significant deviations of *t* and h^2 from zero were identified using a one-sample *t*-test.

Results

Descriptive statistics and trait distribution

The mean feeding potentials of different isofemale mothers did not show statistically significant differences amongst themselves. The individual feeding potential among the isofemale mothers ranged from a minimum of zero to a maximum of 10 mealy bugs per day implying instances do occur when the predator may not feed at all. Mode, the value with the greatest frequency, ranged from two to four mealy bugs per day, with three mealy bugs per day being the most common feeding potential among the isofemale mothers with a range of three mealy bugs per day to a maximum of 10 mealy bugs per day. Similarly, the s^2 was found to be quite high

0.78 to 6.27 (table 1) with high SD showing that the feeding data is widely scattered.

The mean feeding potential of isofemale progenies were lower than their corresponding mothers. However, these progenies differed significantly from each other ($F = 19.004$, $P < 0.0001$) with a mean feeding potential ranging from 1.94 ± 0.05 to 2.95 ± 0.07. The variation in the feeding potential of progenies was less compared to their mothers with a minimum of 1.36 to 4.00 mealy bugs per day. The mode value ranged from 2.07 to 3.33 mealy bugs per day with a range of 0.77 to 2.09. The s^2 and standard deviations were found to be quite lower compared to isofemale mothers ranging from 0.09 to 0.15 and 0.19 to 0.50, respectively implying the feeding data is tightly clustered (table 2).

The frequency of phenotypes of isofemale mothers and their progenies typically varied along a continuous gradient as depicted by a bell curve (figure 1). This clearly shows that the feeding potential in *C. montrouzieri* varied in degree and followed a normal continuous variation distribution pattern which can be attributed to the polygenic effects and the interaction with their environment. Majority of isofemale mothers represented high feeding potential categories compared to their respective progenies. Within the progenies also maximum individuals exhibited lower feeding potential compared to their parents (figure 2) implying the mean phenotypic value for feeding potential decreased in the progenies.

Genetic variation

The genetic parameters studied indicated presence of significant differences among isofemale mothers and progenies. However, significant differences were observed between isofemale progenies ($F = 19.004$, $P < 0.0001$, df 19.580) for feeding potential conveying the genetic variability between isofemale progenies seems to be very high (table 3). Nevertheless, the total phenotypic variance V_p was quite high (4.74) in isofemale mothers compared to their progenies (2.15). The within-line variance (V_w) which harbours mainly nongenetic component (Bell 1997) is very high in isofemale mothers (3.50) compared to the progenies (0.11) which were reared in the laboratory conditions. Interestingly, the between line component was lower in isofemale mothers (1.42) compared to their progenies (2.04) (table 4).

The intraclass correlation coefficient t was also found to be very high in progenies (0.95) compared to isofemale mothers (0.26). The pattern was slightly changed for the coefficients of genetic variation (CV_G) and residual variation (CV_R) in isofemale mothers and progenies. The feeding potential exhibited highest genetic variation (53.14) and lower residual variation (12.34) in progenies and lowest genetic variation (33.87) and higher residual variation in isofemale mothers (12.34) (table 4).

In table 5, the estimates of different measures of genetic variation for feeding potential of individual isofemale progenies are presented. The V_p, V_w, V_b and V_g, which ranged from 3.76 to 9.15, 1.03 to 5.25, 0.61 to 3.90 and 0.49 to 3.73, respectively, among the different isofemale progenies, significantly differed from zero. Regression of isofemale mothers' trait value against their progenies pooled data provided estimate of intercept, 1.68 ± 0.50 and slope of 0.57 ± 0.58. The variability in the progeny feeding potential was explained to the tune of 40 and 63% through linear and polynomial functions and found to be statistically significant ($F = 10$, $P = 0.01$) (figure 3).

Table 1. Descriptive statistics of feeding potential in isofemale mothers.

Isofemale mothers	Mean±SE	Min.–Max.	Range	Median	Mode	σ	s^2
IF1	3.0732 ± 0.25	1.00–10.00	9	3	3	1.57	2.47
IF2	3.3171 ± 0.27	0.00–10.00	10	3	3	1.74	3.02
IF3	3.3171 ± 0.28	0.00–10.00	10	3	3	1.77	3.12
IF4	2.5625 ± 0.40*	0.00– 5.00	5	3	3	1.59	2.53
If5	3.3750 ± 0.22	2.00– 5.00	3	3.5	4	0.89	0.78
IF6	3.4118 ± 0.34	0.00–10.00	10	3	3	1.97	3.89
IF7	3.0000 ± 0.27	1.00– 5.00	4	3	3	1.10	1.20
IF8	3.4706 ± 0.61	0.00–10.00	10	3	2	2.50	6.27
IF9	3.0625 ± 0.36	0.00–6.00	6	3	2	1.44	2.06
IF10	3.3030 ± 0.32	0.00–10.00	10	3	3	1.86	3.47
IF11	3.3684 ± 0.28	2.00–7.00	5	3	3	1.21	1.47
IF12	3.2778 ± 0.24	2.00–6.00	4	3	3	1.02	1.04
IF13	3.3438 ± 0.38	0.00–10.00	10	3	3	2.13	4.56
IF14	3.5294 ± 0.52	0.00–10.00	10	3	3	2.15	4.64
IF15	3.3200 ± 0.43	0.00–10.00	10	3	3	2.14	4.56
IF16	3.2800 ± 0.40	0.00–10.00	10	3	3	2.01	4.04
IF17	3.1200 ± 0.40	1.00–10.00	9	3	3	2.01	4.03
IF18	3.2174 ± 0.48	0.00–10.00	10	3	3	2.32	5.36
IF19	4.1250 ± 0.61*	1.00–10.00	9	3	3	2.45	5.98
IF20	3.2941 ± 0.56	0.00–10.00	10	3	4	2.31	5.36

*Significant at $P = 0.04$.

Table 2. Descriptive statistics of feeding potential in isofemale progenies.

Isofemale progenies	Mean±SE	Median	Mode	σ	s^2	Range	Min.–Max.
IFP1	2.952 ± 0.065	2.95	2.67	0.35	0.13	1.68	2.27–3.94
IFP2	2.820 ± 0.063	2.81	3.00	0.34	0.12	1.68	2.20–3.88
IFP3	3.173 ± 0.058	3.22	3.30	0.32	0.10	1.55	2.20–3.75
IFP4	1.941 ± 0.053	1.96	2.07	0.29	0.09	1.29	1.36–2.64
IFP5	2.796 ± 0.062	2.80	2.61	0.34	0.12	1.55	2.09–3.64
IFP6	2.625 ± 0.034	2.61	2.61	0.19	0.04	0.77	2.24–3.00
IFP7	2.814 ± 0.053	2.76	2.91	0.29	0.08	1.15	2.40–3.55
IFP8	2.682 ± 0.092	2.63	2.13	0.50	0.25	2.09	1.91–4.00
IFP9	2.736 ± 0.066	2.71	2.71	0.36	0.13	1.50	1.92–3.42
IFP10	2.545 ± 0.052	2.56	2.42	0.29	0.08	1.01	2.05–3.06
IFP11	2.826 ± 0.068	2.80	2.55	0.38	0.14	1.52	2.12–3.64
IFP12	2.798 ± 0.055	2.77	2.83	0.30	0.09	1.41	2.12–3.52
IFP13	2.923 ± 0.060	2.90	3.33	0.33	0.11	1.28	2.32–3.60
IFP14	2.875 ± 0.071	2.84	3.19	0.39	0.15	1.38	2.25–3.63
IFP15	2.662 ± 0.050	2.67	2.87	0.27	0.08	1.07	2.13–3.20
IFP16	2.614 ± 0.056	2.51	2.35	0.31	0.09	1.26	2.18–3.44
IFP17	2.639 ± 0.038	2.64	2.59	0.21	0.04	0.87	2.19–3.06
IFP18	2.634 ± 0.070	2.52	2.75	0.38	0.15	1.40	2.13–3.53
IFP19	2.405 ± 0.055	2.39	2.44	0.30	0.09	1.56	1.75–3.31
IFP20	2.305 ± 0.054	2.32	2.29	0.30	0.09	1.35	1.71–3.06

The differences between progeny mean values are significant at $P < 0.0001$; CD = 0.17; $F = 19.004$; df 19,580.

The intraclass correlation coefficient t which is used to estimate the genetic variability with an isofemale design ranged between 0.11 and 0.56 and was significantly different among the progenies, though the direction of differences between isofemale progenies was not consistent. The heritability estimates h^2, (isofemale heritability) which is calculated from intraclass correlation coefficients (t) for different isofemale progenies ranged from 0.22 to 1.12 and clearly t seemed closer to 0.5 (h^2) (table 5).

The correlation of overall genetic variation with phenotypic trait values exhibited very strong statistically significant relation with isofemale progenies (r = 0.63) than mothers (r = 0.01). On the contrary, the nongenetic variation showed significant correlation with isofemale mothers (r = 0.70**) compared to their progenies (r = 0.28). The total phenotypic variation showed a significant relation with trait value with both isofemale mothers (r = 0.49*) and their progenies (r = 0.53*). Plotting total phenotypic variation against variance components showed significant contribution by V_g (F = 16.90, $P < 0.001$) and V_e (F = 83.67, $P < 0.0001$). However, contribution of environmental variation was found to be higher ($R^2 = 0.8311$) compared to genetic variation ($R^2 = 0.4986$) (figure 4).

Discussion

Genetic variation in the feeding potential of adult *C. montrouzieri* was studied using 20 random isofemale lines collected from Bangalore, India. The heritability of feeding potential was estimated through isofemale heritability (t) and parent–offspring regression. The results indicated that the feeding potential in 90% of isofemale mothers did not differ significantly from each other except for two out of 20 comparisons. However, the variability in the feeding of isofemale mothers was found to be higher. The exception was

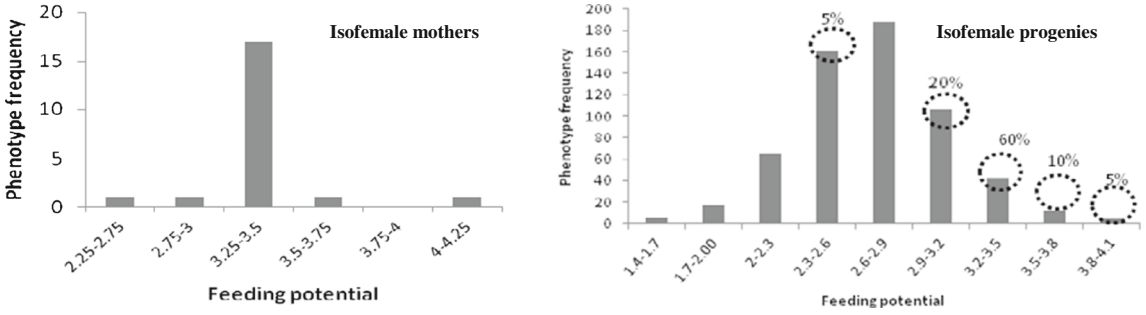

Figure 1. Distribution of mean frequencies of phenotypes based on feeding potential in isofemale mothers and their progenies. The dotted circles represent the percentage of isofemale mothers belonging to respective feeding potential categories.

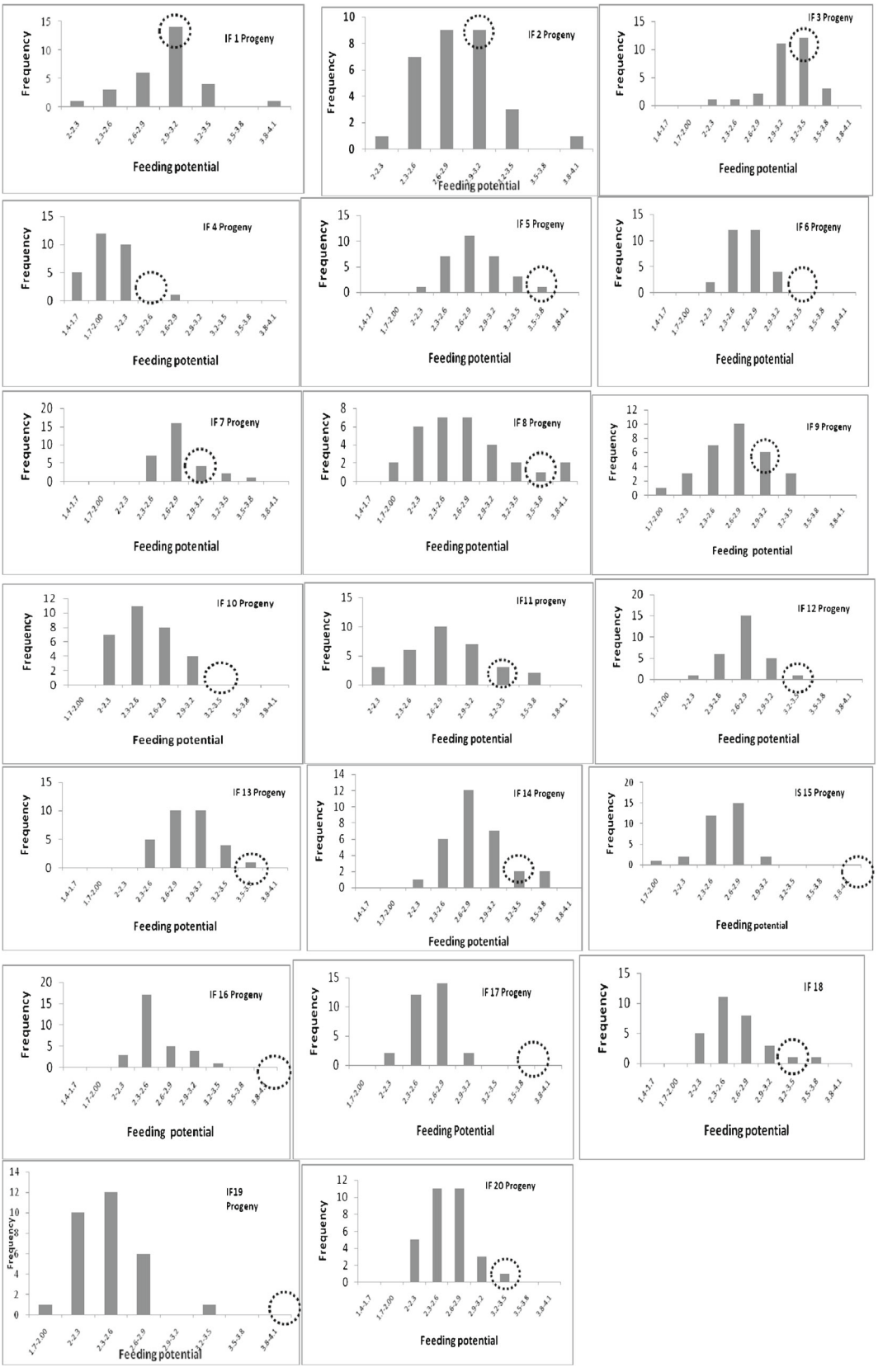

Figure 2. Distribution of phenotype frequencies for feeding potential in each isofemale progeny. From each progeny 30 individuals were observed continuously for 15 days. The dotted circles represent the feeding potential category to which the respective isofemale mother belongs.

Table 3. One-way ANOVA of feeding potential of *C. montrouzieri* in 20 isofemale mothers and their progenies.

Exp. population	Source of variation	df	MS	*F*
Isofemale mothers	Among lines	19	1.421	0.406 ($P = 0.988$)
	Within lines	468	3.501	–
Isofemale progenies	Among progenies	19	2.043	19.004 ($P<0.0001$)
	Within progenies	580	0.108	–

the difference between the feeding potential of isofemale mother 4 and 19 which were found statistically different (table 1). But majority conformed to a set pattern of feeding potential. The phenotype frequency distribution for feeding potential among isofemale mothers as well as their progenies followed a typical bell curve showing the non-mendelian inheritance of this trait that created a continuum of phenotypes showing the quantitative nature. A phenotypic distribution such as this is consistent with most polygenic trait models of natural population (Thompson and Taylor 1985). Further, a continuous distribution is commonly considered strong evidence for a broad range of underlying genotypes produced by segregation at many loci (Thompson and Taylor 1985) or suggestive of only a few genes or gene complexes that are segregating (Thoday and Thompson 1976).

The feeding potential of isofemale progenies was reduced compared to their mothers, though they did differ significantly among themselves (table 2). The phenotypic variance was higher in isofemale mothers and lower in their progenies which were reared under conducive conditions. The phenotypic variation results from several factors: the underlying genetic differences among insects and the environment to which the insect is exposed. Natural populations experience heterogeneous environments where local conditions vary temporally and spatially (Weinig and Schmitt 2004) and these in turn exert performance trade-offs on quantitative traits in term of phenotypic variation as observed in the present study.

Nevertheless, the estimates of genetic variation were generally higher in isofemale progenies than their mothers. The increased heritabilities and genetic variances in isofemale progenies may be associated with a more substantial reduction of nongenetic components due to laboratory rearing as optimal rearing conditions favour and may be a prerequisite for a high genetic repeatability.

The high phenotypic variance V_p in isofemale mothers compared to their progenies may be due to increase in within line component (V_w) or environmental component of phenotypic variation. Ecologists often consider that the within-line variance harbours mainly a nongenetic component (Bell 1997; David *et al*. 2005), i.e., $V_w \approx V_e$. On the contrary, reduced V_p was observed among the isofemale progenies with corresponding huge reduction in V_w and substantial increase in genetic variance (table 4). Recently, much of the focus has been on whether unfavourable versus favourable conditions increase or decrease the genetic variation (Hoffman and Merila 1999) and the hypotheses supporting both the situations do exist. Both V_b and V_w varied in different directions both in isofemale mothers and their progenies. The fact that V_b and V_w may vary in opposite ways was recently demonstrated (Petavy *et al*. 2004) in lines submitted to a daily thermal stress where both cold and heat stress increased the within (environmental) variance, but opposite results were obtained for the between-line (genetic) variance. As observed in the present study where increase in the genetic variation was observed in the first generation of laboratory reared isofemale progenies implying uniform favourable conditions increases the genetic variation by bringing down the V_e compared to the isofemale mothers where the exact contrary was observed. Under unfavourable conditions, a relatively large decrease in heritability was observed for development time in *Drosophila melanogaste*r Meigen (Imasheva *et al*. 1998) and for fecundity in cotton-stainer bugs, *Dysdercus fasciatus* (Kasule 1991) where the decrease was associated with lowered genetic variance as observed in the present study.

The heritability of feeding potential estimated by parent–offspring regression ($h^2 = 1.40$; figure 3) was lower than the overall heritability estimated by isofemale lines ($h^2 = 1.90$). This may be explained as isofemale design is a modification of the full-sib design where the full-sib covariance includes additive as well as nonadditive variance components in addition to components due to dominance and epistasis (Falconer and Mackay 1996). Further, the parent–offspring covariance does not include the dominance components and includes a

Table 4. Means, variance components, heritabilities, intraclass correlation and coefficients of variation for feeding potential. The total number of individuals used was 600 from 20 isofemale progenies and 20 isofemale mothers (analysis on 15 days observations for each individual).

Exp. Population	Mean feeding potential ($n = 450$)	V_p	V_w	V_b	V_g	*t*	CV_G	CV_R
Isofemale mothers	3.288 ± 0.064 (*R* 2.56–4.13)	4.74	3.50	1.42	1.24	0.262	33.87	56.90
Isofemale progenies	2.688 ± 0.058 (*R* 1.94–3.17)	2.15	0.11	2.04	2.04	0.949	53.14	12.34

Table 5. Variance components, heritabilities, intraclass correlation and coefficients of variation for feeding potential in different isofemale progenies. The total number of individuals used was 30 from each 20 isofemale progenies (analysis on 15 days observations for each individual).

Isofemale progenies	V_p	V_w	V_b	V_g	h^2	t	Var(t)	CV_G	CV_R
IFP1	5.18	3.20	2.05	1.98	0.74	0.37*	0.009	47.66	60.59
IFP2	5.37	3.55	1.83	1.71	0.63	0.32*	0.009	46.37	67.84
IFP3	5.92	4.33	1.59	1.45	0.48	0.24	0.007	37.95	66.64
IFP4	2.37	1.03	1.35	1.31	1.11	0.56**	0.009	58.96	53.04
IFP5	6.11	4.18	1.93	1.79	0.58	0.29*	0.008	47.86	74.35
IFP6	4.09	3.49	0.61	0.49	0.22	0.11	0.003	26.72	72.42
IFP7	4.47	3.34	1.13	1.02	0.44	0.22	0.006	35.89	66.01
IFP8	9.15	5.25	3.90	3.73	0.82	0.41**	0.010	72.01	86.81
IFP9	5.25	3.43	1.82	1.70	0.65	0.32*	0.009	47.66	68.88
IFP10	5.43	3.52	1.91	1.79	0.66	0.33*	0.009	52.57	74.96
IFP11	6.56	4.17	2.39	2.25	0.69	0.34*	0.009	53.09	73.48
IFP12	5.30	3.62	1.68	1.56	0.59	0.29*	0.008	44.64	69.13
IFP13	5.46	3.31	2.16	2.05	0.75	0.38*	0.010	48.98	63.17
IFP14	7.82	5.16	2.66	2.48	0.63	0.32*	0.009	54.77	80.37
IFP15	5.23	3.24	1.98	1.87	0.71	0.36*	0.009	51.37	68.86
IFP16	6.01	3.72	2.30	2.17	0.72	0.36*	0.009	56.36	74.98
IFP17	5.30	4.04	1.25	1.12	0.41	0.21	0.006	40.11	77.49
IFP18	6.64	4.25	2.39	2.25	0.68	0.34*	0.009	56.94	79.54
IFP19	5.08	2.19	2.88	2.81	1.12	0.56**	0.009	69.70	62.65
IFP20	3.76	1.78	1.97	1.92	1.03	0.51**	0.010	60.12	58.85

The differences between family mean values are significant at $P < 0.0001$; CD = 0.17; $F = 19.004$; df 19,580); t significance (*$P < 0.05$, **$P < 0.001$).

far lesser proportion of the epistatic variance (Bubliy *et al*. 2001) implying if the dominant and epistatic components constitute a large part of the genetic variance, estimates of genetic variation in isofemale lines should be greater than parent–offspring estimates as observed in the present study. However, it is possible that inbreeding may also enhance among-line variation (Bubliy *et al*. 2001) and to obtain meaningful heritabilities, isofemale lines must be tested within five generations after establishment (Hoffmann and Parsons 1988). In the present study, the heritability was estimated in the first laboratory generation itself and which are non-inbred ruling out the possibility of inbreeding as a cause for increased heritability. This further endorses the influence of dominance/epistasis components in the heritability of feeding potential in the isofemale progenies.

The intraclass correlations (t) were found to be statistically significant in 15 out of 20 progenies and the heritability estimates (h^2) in these progenies were high (0.58–1.12) showing the genetic influence on feeding potential of *C. montrouzieri*. Usually the heritability estimates determine the magnitude of genetic influence on behavioural traits, however inherent flexibility do occur due to learning (Blanckenhorn and Perner 1994). Thus, unless the degree to which animals learn is under genetic control, heritability estimates of foraging traits

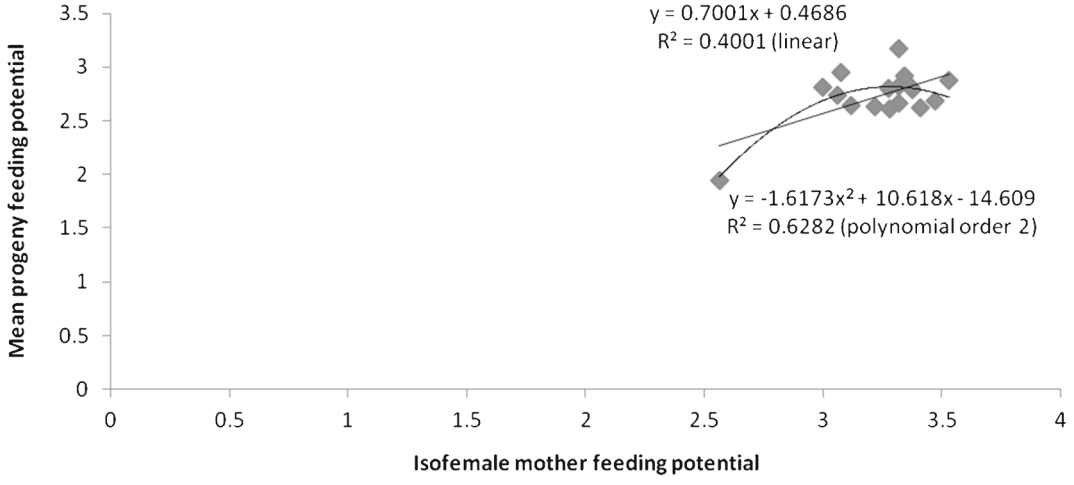

Figure 3. Relationship between feeding potential of isofemale mothers and their progenies.

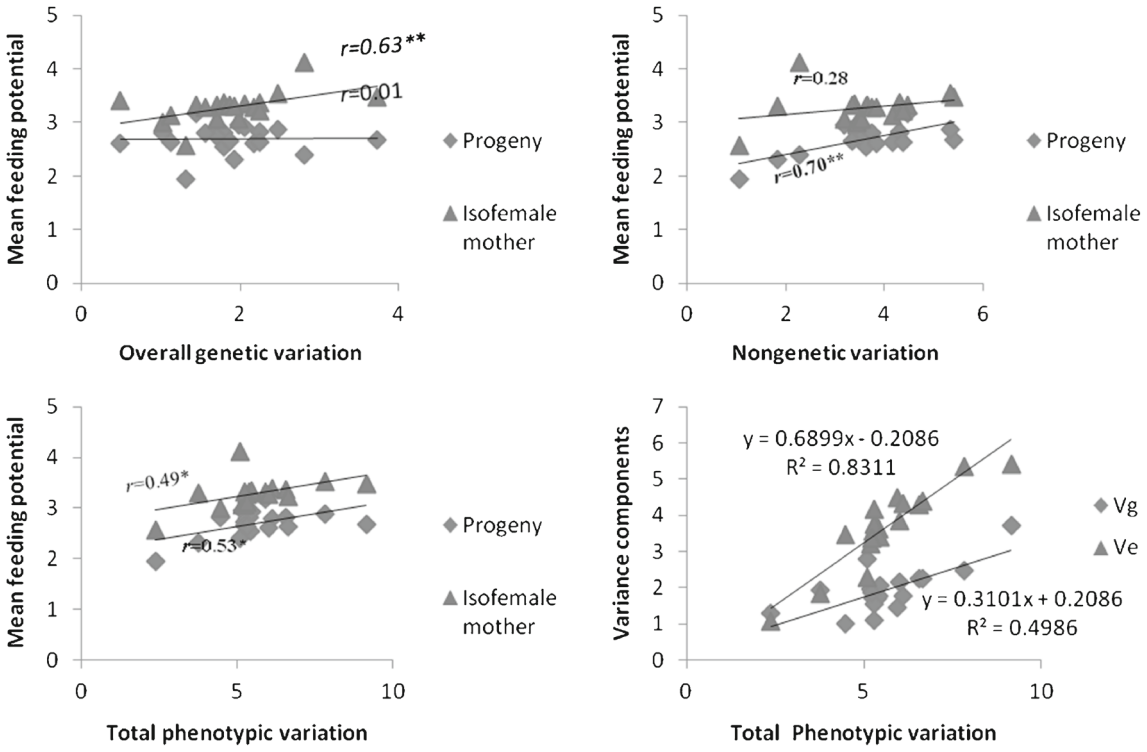

Figure 4. Relationship between different variance components in isofemale mothers and their progenies.

should be low when calculated from experienced individuals; learning may transcend most genetic effects on foraging behaviour and thus heritabilities that are calculated from such behaviours may be deflated (Blanckenhorn and Perner 1994). In the present study, the heritability estimates were calculated from the first laboratory generation adults that too immediately after eclosion ruling out any learning. Nevertheless, the importance of isofemale technique as a basic tool for sampling a natural population to understand quantitative and ecological genetics often obscured with some limitations for heritability measurements. The relationship between the more usual heritability and the intraclass correlation is not straight forward, presumably because the foundation of each line unravels a large amount of epistatic interactions, which otherwise would remain cryptic in a large panmictic population. Further sampling of genetically related natural populations (e.g. progeny from the same mother) leads to the sampling of a given chromosome more than once (David *et al*. 2005).

The variability in the feeding potential of isofemale progenies was explained to the extent of 40% (linear) and 63% (polynomial) suggesting considerable quantitative variation and existence of population differences. In general, these results indicated that the populations may possess higher inherent variability that was passed on to them from their mothers. Thus, parental phenotypic and genetic differences may be related to progeny genetic variance and heritability. This was supported by the strong correlation of overall genetic variation with phenotypic trait values in isofemale progenies (figure 4) suggesting this trait may be controlled by fewer genes, with greater additive gene action. This gives clue that during mass rearing programmes of *C. montrouzieri*, the ability to identify parental combinations that will result in greater progeny genetic variance and heritability would help to maximize the genetic gain from selection. Similarly, the QTL mapping studies for feeding potential of this predatory coccinellid would be made more efficient if parent combinations resulting in greater progeny genetic variances could be determined before investing resources in mapping population development. Nongenetic variation exhibited a very strong correlation with isofemale mothers than their progenies as expected. Though, both variance components (V_g/V_e) contributed significantly to the total phenotypic variation, the overall contribution of environmental variance is higher than the genetic component conveying the bigger role of environment in deciding the phenotypic expression of given genotype via genotype–environment interactions. The interactions between genotype and environment reflect specialization via adaptation and have been demonstrated in several other systems (Via 1984, 1986, 1990). However, this study had limited power to test this relationship as V_g as measured by the isofemale technique is not the additive genetic variance, but V_{ga} is likely to include dominance and epistatic effects (David *et al*. 2005).

The differences observed for the feeding potential between isofemale progenies reflect the underlying genetic influence

of this trait and its biological significance. Parental phenotypic and genetic differences in feeding potential are related to progeny genetic variance and heritability. Both additive and nonadditive genetic effects were important determinants of phenotypic variation in feeding potential of *C. montrouzieri*. Further, the values of genetic coefficients of variation showed that the additive effect is stronger compared to nonadditive effect. More detailed studies are needed in this direction to offer clear insights into the genetic and ecological circumstances that determine the relative sensitivity of genotype to the forces of drift and selection.

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