

Variations of Reproductive Traits of Two Semi-terrestrial Isopods, *Ligia exotica* and *L. taiwanensis* (Crustacea: Ligiidae), in Southern Taiwan

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Dept. of Zoology, National Taiwan Univ., Taipei, Taiwan 106, R.O.C. Tel: 886-2-363-0231 ext. 3324, Fax: 886-2-3638554,
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Min-Li Tsai, Hon-Cheng Chen (1997) Variations of reproductive traits of two semi-terrestrial isopods, *Ligia exotica* and *L. taiwanensis* (Crustacea: Ligiidae), in southern Taiwan. *Zoological Studies* 36(1): 33-41. Both inter- and intraspecific reproductive traits of 2 semiterrestrial isopods were examined and compared in an attempt to provide insights into the adaptive strategies of reproduction. Gravid females of *Ligia exotica* (Roux) from the littoral zone and *Ligia taiwanensis* (Lee) from mountain brooks show differences in reproductive allocation per brood ($F_{1,198} = 706, p < 0.001$), weight-specific egg weight ($F_{1,198} = 166, p < 0.001$), and weight-specific fecundity ($F_{1,198} = 120, p < 0.001$), but they also display similarities in the interrelationships between reproductive traits.

The reproductive traits of *L. taiwanensis*, such as larger weight-specific egg size and lower reproductive allocation, seem more in accordance with theoretical predictions for *K*-selected traits than those of *L. exotica*. When the effects of body size are removed, both species show a significant positive correlation between fecundity and brood weight (*L. exotica*: $r = + 0.49, t = 5.50, p < 0.001$; *L. taiwanensis*: $r = + 0.96, t = 36.09, p < 0.001$), and a negative correlation between fecundity and egg size (*L. exotica*: $r = - 0.77, t = 11.78, p < 0.001$; *L. taiwanensis*: $r = - 0.32, t = 3.41, p < 0.001$) intraspecifically. The reciprocal relationships between egg size and fecundity in *L. exotica* and *L. taiwanensis* seem to match the assumption of optimality theories of life-history evolution.

Key words: *Ligia*, Reciprocal relationship, Life-history evolution.

Ligia exotica is a common, widely distributed semiterrestrial species in the supralittoral zone of sheltered and exposed coasts around Taiwan (Chen 1987). In contrast, *L. taiwanensis* is only found on the banks of mountain brooks on the Hengchuen Peninsula in southern Taiwan. The resemblances in morphology and taxonomic relationship between these 2 species have been noted by Lee (1994).

Life history patterns and reproductive traits of crustaceans in the same or different environments are extremely variable (Sastry 1983). Warburg (1994) investigated 7 species of terrestrial isopods inhabiting 3 types of habitats and found no positive relationship between the reproductive patterns and their anatomy, taxonomy, or ecological conditions

within their habitats. Different isopod species with specific morphological constraints may evolve different strategies. The survival and reproduction of an organism are a function of its particular ecological setting, as governed by the effects of mechanical and physiological constraints. Thus ecological constraints form the backdrop for all life history (Roff 1992).

There have been some studies on intraspecific variations in isopod life histories (Sunderland et al. 1984, Warburg 1987, Souty et al. 1994). It is conceivable that species with close taxonomic relationships that are similar in morphology and physiology would evolve different reproduction strategies in response to constraints of different environmental challenges. Intraspecific correlation

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among traits may also elucidate the questions of what combinations of traits will be favored in the long run (Roff 1981 1992). Studies of the variations of reproductive traits of *L. exotica* and *L. taiwanensis* may provide an insight into the evolution of life-history strategies under close taxonomic relationships and similar physio-morphological constraints. In this study, the reproductive traits within and between 2 *Ligia* species in southern Taiwan are examined and compared, and an attempt is made to elucidate the reproductive strategies of these 2 species in their habitats.

MATERIALS AND METHODS

The climates of the Hengchuen Peninsula are typical of tropical islands where the temperature and humidity remain at high levels all year round. *Ligia exotica* and *L. taiwanensis* which inhabit this area breed throughout the year. *L. taiwanensis* females with brood pouches were collected from the banks of mountain brooks about 1 km inland from the seashore. Specimens of *L. exotica* were collected from the littoral zone of the rocky shore of the Hengchuen Peninsula. Specimens were transported in tanks containing the moist substratum from their natural habitat, and covered by a plastic plate to maintain high humidity. Specimens were maintained in the laboratory for 2 days to clean the guts before measurements were taken.

An index of mean reproductive allocation per brood for individual species based on the weight of emerging juveniles has been proposed by Sutton et al. (1984). The index based on the egg weight as substituted for the weight of the juvenile was used by Ma et al. (1991), because the deposition of calcium carbonate during exoskeleton formation may have an overwhelming effect on the weight of emerging juveniles.

The animals were killed by chilling with refrigeration. For the ova count, females were dissected in distilled water. The contents of the brood pouch were removed and counted, and the ova were placed on a glass pan for later dehydration. To get an unbiased egg weight, great care was taken not to damage the eggs during the dissection operations. Pandian (1972) divided the embryonic period of development into 4 stages on the basis of color and morphology of eggs of *Ligia oceanica*. In the later stage of embryonic development, the egg weight increased due to the absorption of nutrients from the brood pouch environment (Pandian 1972). To avoid the source of error caused by difference

in developmental stages, the eggs were examined under a microscope. Only broods showing no signs of development and eggs with globular form and light color upon external examination were used. Eggs and body were dried in an oven at 100 °C for 48 h, and dry weights of body, brood, and eggs were weighed to 0.01 mg. To reduce the error caused by varying water content, dry weights were used for all calculations and analyses.

Regression models were used to describe the relationships among female body size, brood weight, fecundity, and average egg weight. The variability between reproductive characteristics of 2 species collected from different habitats was analyzed by ANCOVA, partial correlation, and multiple regression (Nie et al. 1975, Sokal and Rohlf 1981, Zar 1984). Path analysis is an appropriate method for studies of cause and effect among variables which are interrelated and not independent (Sokal and Rohlf 1981). It is applied here to elucidate the hypothesis of the causality between the variables.

RESULTS

Comparison of reproductive traits

The reproductive traits showed differences between *Ligia exotica* (Roux) from the littoral zone and *L. taiwanensis* from a mountain brook. The maternal body size, brood weight, fecundity, and egg size of *L. exotica* were larger than those same features of *L. taiwanensis* (Table 1). The weight-specific fecundity and egg weight of *L. taiwanensis* were relatively larger than those of *L. exotica*. In contrast, the reproductive allocation per brood of *L. taiwanensis* was relatively smaller than that of *L. exotica* (Table 1).

The effects of body size

In both species, the relationships between body size and brood weight, and fecundity and egg size were all significant (Table 2). The regression equation is shown in Fig. 1. Both species showed a significant positive relationship between body size and brood weight, fecundity, and egg weight. The parallelism tests also showed that the regression slopes of brood weight and fecundity versus female size were significantly different between 2 populations (brood weight: $F_{1,198} = 10.61, p < 0.001$; fecundity: $F_{1,198} = 47.93, p < 0.001$). A similar slope ($F_{1,198} = 0.03, NS$) was found in egg size

versus body size for both *L. exotica* and *L. taiwanensis*, yet the respective intercepts were quite different (Table 2; Fig. 1). It seems likely that the size of eggs produced is constrained by the body size of each species.

Within a species, part of the variations in egg size and fecundity could be explained by the maternal size. However, a large amount of variation in egg weight remained unexplained by body size in both species (*Ligia exotica*: 67%; *L. taiwanensis*: 75%), and a substantial amount of fecundity variation remained unexplained (*L. exotica*: 12%; *L. taiwanensis*: 27%). These residual variations in reproductive traits may have important implications for, or be related to individual fitness.

Effects other than body size

The effects of body size on reproductive traits of each species were removed statistically. The

partial correlation coefficient (Table 3) showed a highly significant positive correlation between fecundity and brood weight in both species (*L. exotica*: $r = + 0.49$, $t = 5.50$, $p < 0.001$; *L. taiwanensis*: $r = + 0.96$, $t = 36.09$, $p < 0.001$). This suggests that individuals with greater reproductive allocation produce more eggs when the effect of body size is removed. A significant negative correlation was also present between weight-specific fecundity and egg weight in both species (*L. exotica*: $r = - 0.77$, $t = 11.78$, $p < 0.001$; *L. taiwanensis*: $r = - 0.32$, $t = 3.41$, $p < 0.001$). This indicates that an increase of weight-specific fecundity is also associated with smaller eggs. A reciprocal relationship exists between fecundity and egg size in each species. No significant correlation was found between egg size and brood weight in either *L. exotica* or *L. taiwanensis* (Table 3) which indicates that egg weight does not vary with the variation of reproductive allocation when the factor

Table 1. Mean and coefficient of variation (CV) of weight-specific and absolute brood dry weight (mg), fecundity (number of eggs) and egg dry weight (mg), and ANOVA results between *Ligia exotica* (e.) ($n = 100$) and *Ligia taiwanensis* (t.) ($n = 102$)

Reproductive characteristics	Mean		CV		Between species		
	(t.)	(e.)	(t.)	(e.)	df	F	p
Absolute:							
Body size	19.02	53.18	28.18	19.26	1, 200	887.14	< 0.001
Brood weight	2.60	10.44	31.15	19.54	1, 200	1 294.41	< 0.001
Fecundity	22.16	50.39	29.42	16.93	1, 200	669.88	< 0.001
Egg weight	0.12	0.21	6.42	6.00	1, 200	4 329.29	< 0.001
Weight-specific:							
Reproductive allocation	0.14	0.20	14.28	3.50	1, 200	705.76	< 0.001
Fecundity	1.17	0.95	11.11	6.58	1, 200	119.64	< 0.001
Egg weight	0.006	0.004	28.75	17.50	1, 200	166.01	< 0.001

Table 2. Summary of ANCOVA result of the relationship between body dry weight and brood weight, fecundity, and egg dry weight for *Ligia exotica* (e.) ($n = 100$) and *Ligia taiwanensis* (t.) ($n = 102$)

Characteristics	Source of variation	df	F	p
Brood weight:	Regression (e.)	1, 98	2 901.79	< 0.001
	Regression (t.)	1, 100	364.94	< 0.001
	Between slopes (e. & t.)	1, 198	10.60	< 0.005
Fecundity:	Regression (e.)	1, 98	737.11	< 0.001
	Regression (t.)	1, 100	275.60	< 0.001
	Between slopes (e. & t.)	1, 198	47.93	< 0.001
Egg weight:	Regression (e.)	1, 98	47.58	< 0.001
	Regression (t.)	1, 100	33.74	< 0.001
	Between slopes (e. & t.)	1, 198	0.03	NS

NS: not significant at $p > 0.05$.

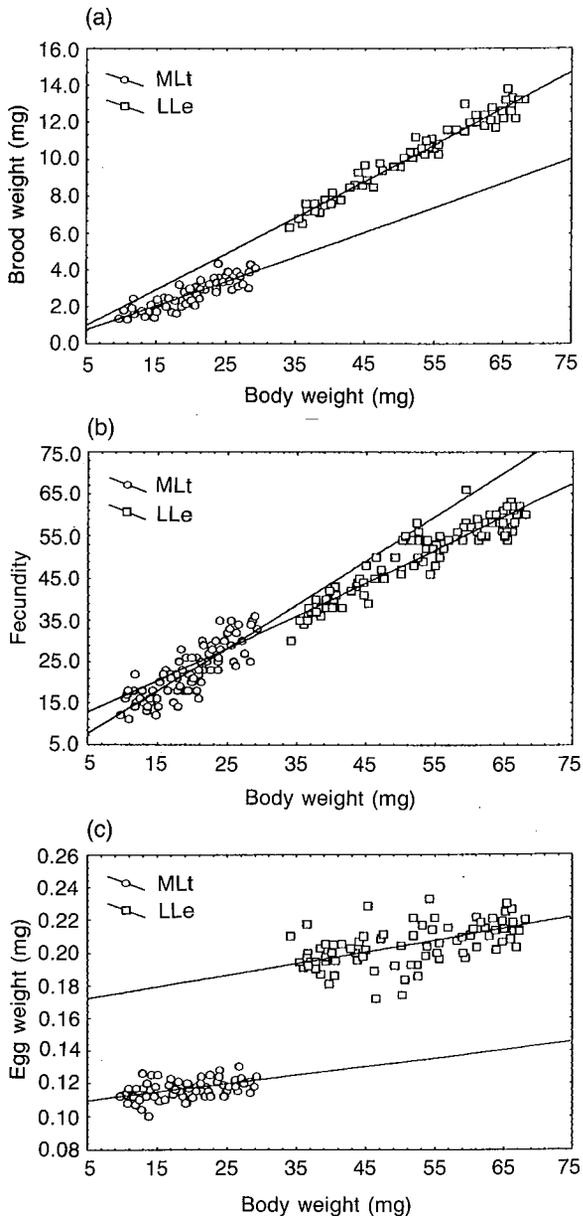


Fig. 1. Relationship between female size and (a) brood dry weight, (b) fecundity, and (c) egg dry weight for *Ligia exotica* from the littoral zone (LLe) and *L. taiwanensis* from a mountain brook (MLt). Regression equations are: (a) *L. exotica*: $y = -0.0008 + 0.1963x$; *L. taiwanensis*: $y = -0.0609 + 0.1334x$; (b) *L. exotica*: $y = 8.7648 + 0.7827x$; *L. taiwanensis*: $y = 2.3474 + 1.0418x$; (c) *L. exotica*: $y = 0.1691 + 0.0007x$; *L. taiwanensis*: $y = 0.1070 + 0.0005x$.

of body size is removed.

Path diagrams of interrelationship among the traits

Path analysis and stepwise multiple regression

were carried out to interpret the interrelationships between causes and apparent effects, and the amount of variation that could be explained by other variables in a causal hierarchy, respectively. The effect of any presumptive causal variables (female dry weight and the material allocated to the brood) on criterion variables (fecundity and egg size) was evaluated. The causal variables were entered into the model in a hierarchy based on time precedence or sequence. For example, body size was taken as affecting brood weight through growth, and it entered the model before reproductive allocation. The variables that explain a non-significant part of the residual variations were excluded. For instance, brood weight (reproductive allocation) was less related to egg size in *L. exotica* (Table 3), and was thus excluded in the model of egg size. The reciprocity between egg size and fecundity was included as the last step in multiple regressions. The path diagrams that represent an explicit hypothesis of the causality between the variables are shown in Fig. 2. The arrows and the path coefficients (the standardized partial regression coefficients) indicate the direction and the magnitude of causality, respectively. Table 4 demonstrates the total amount of variation in fecundity and egg size explained by the model. The residual variations of each hierarchy in path analysis model is taken as the estimate of the magnitude of unknown factors affecting the criterion variable (U1 to U3) in each step (Fig. 2).

The structures of the path diagrams are similar between the 2 species. Body size has a direct positive effect on egg size (+1.44) (larger individuals produced larger eggs) in *L. exotica*. In the analysis of fecundity, the correlative effects of body size revealed two significant and positive components, one direct (+1.14) and one through an effect on reproductive allocation (0.0388×0.2155), yet the indirect effect is very small relatively to the direct one. Brood size also varied positively with fecundity ($0.2155 - 0.2155 \times 0.0388$). A similar pattern was found in *L. taiwanensis* (Fig. 2b). In *L. taiwanensis*, the path coefficient (Fig. 2b) shows that body size is more important in affecting the size of eggs than the reciprocal effects by fecundity. This result corresponds with the result of the analysis of variance (Table 4) in that the reciprocal effects explains a relatively smaller part of total egg size variation than that of body size. It indicates that body size plays a more important role in affecting the size of eggs (smaller or larger) than the reciprocal relationships between fecundity and egg size.

Table 3. Summary of 1st order partial correlation analysis between fecundity, egg size, and brood weight of *Ligia exotica* and *L. taiwanensis*, when the effect of body weight has been removed

Species		<i>r</i>	<i>t</i>	<i>p</i>
<i>Ligia exotica</i> :	Fecundity & brood weight	+ 0.4874	5.4979	< 0.001
	Fecundity & egg weight	- 0.7673	11.7824	< 0.001
	Egg weight & brood weight	+ 0.1678	1.6766	NS
<i>Ligia taiwanensis</i> :	Fecundity & brood weight	+ 0.9640	36.0872	< 0.001
	Fecundity & egg weight	- 0.3238	3.4055	< 0.001
	Egg weight & brood weight	- 0.0732	0.7300	NS

NS: not significant at $p > 0.05$

Fig. 3 presents the relationships between female body size and fecundity and mean weight of young for several species of isopods. It also shows that the larger species produce more and larger offspring.

Explanation of variations

About 99.7% of fecundity variations and 72.0% of egg size variations in *L. exotica* are explained by this additive model. In *L. taiwanensis*, 98.0% of the fecundity variations and only 33.0% of the egg weight variations were explained (Table 4). The low explanation of egg size variation reflects the importance of unknown factors which affect the size of eggs for *L. taiwanensis* inhabiting mountain brooks. The magnitudes of the unknown factors, with U1 being much larger than U2 in both species

(Fig. 2), are in accordance with the results of variation explanations. Besides, the unknown factors affecting reproductive allocation (U3) are also important.

DISCUSSION

Interspecific variations

Females of *L. taiwanensis* produce fewer and smaller eggs than females of *L. exotica*. Fig. 3 displays the fecundities and sizes of young relative to body size for 9 species of terrestrial or semi-terrestrial isopods. Either the fecundity or the size of young increases with an increase of body size in both species. These breeding characteristics also vary for marine, freshwater, and terrestrial isopods (Carefoot 1973). Geographic differences also exist in size at maturity and the number of eggs within a given group of isopods (Sastry 1983). Semi-terrestrial and terrestrial decapods that seek marine water and freshwater for breeding purposes also show variations in their reproductive strategies (Sastry 1983). Those species that return to the sea to release larvae produce a large number of small eggs as marine forms (Bliss 1968 1979). In contrast, freshwater species produce large eggs, which directly develop to hatch young as miniature adults (Koba 1936).

Intraspecific interrelationships among the traits

Intraspecific variations in life-history parameters have been demonstrated in isopods such as the terrestrial species, *Armadillidium vulgare* (Lawlor 1976a, b, Miller and Cameron 1983, Brody and Lawlor 1984), and the semi-terrestrial species, *Ligia oceanica* (Willows 1978a, b). The partial correlation

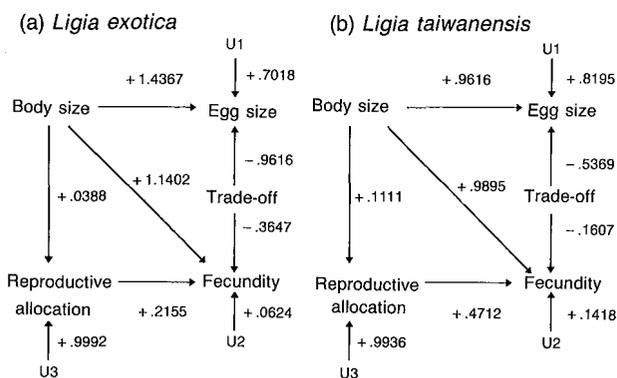


Fig. 2. Path diagrams and path coefficients of body size and reproductive allocation affecting fecundity and egg size for (a) *Ligia exotica* and (b) *L. taiwanensis*. Path coefficients and arrows indicate the magnitude of the effect and the direction, respectively. U1, U2, and U3 are unknown factors affecting egg size, fecundity, and reproductive allocation in the hierarchical model, respectively.

Table 4. Analysis of the components of variation of fecundity and egg size in *Ligia exotica* from a littoral zone and *L. taiwanensis* from a mountain brook

Source of variation	<i>Ligia exotica</i>					<i>Ligia taiwanensis</i>				
	df	SS	F	p	P(%)	df	SS	F	p	P(%)
Fecundity:										
Body size	1	6 360.19	737.11	< 0.001	88.26	1	3 146.48	275.60	< 0.001	73.38
Allocation	1	190.94	28.29	< 0.001	2.65	1	976.16	1 456.97	< 0.001	22.76
Trade-off	1	634.05	2 949.09	< 0.001	8.80	1	80.47	92.70	< 0.001	1.88
Unexplained	96	20.68				98	85.06			
Explained	3	7 185.11	11 119.42	< 0.001	99.71	3	4 203.11	1 614.09	< 0.001	98.02
Total	99	7 205.79				101	4 288.17			
Egg size:										
Body size	1	0.0051	47.58	< 0.001	32.48	1	0.00077	33.74	< 0.001	25.16
Trade-off	1	0.0062	138.45	< 0.001	39.49	1	0.00024	12.00	< 0.001	7.85
Unexplained	97	0.0043				99	0.00205			
Explained	2	0.0113	126.66	< 0.001	71.97	2	0.00101	24.46	< 0.001	33.01
Total	99	0.0157				101	0.00306			

P(%): Percentage of total variation that was explained by each variable.

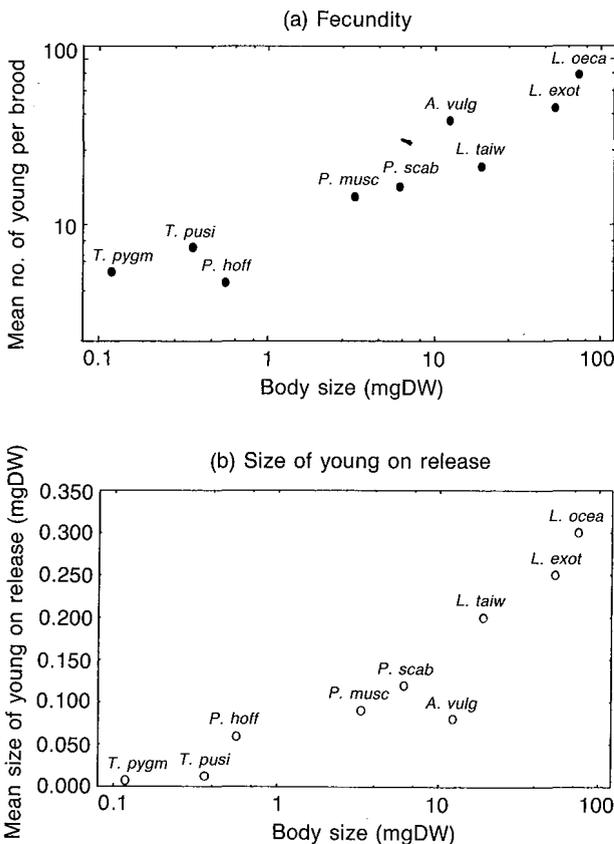


Fig. 3. The relationship between mean body weight and (a) fecundity, and (b) mean weight of each individual young on release. The source data of fecundity and mean size of young for *Platyarthrus hoffmannseggii* (*P. hoff*), *Trichoniscus pygmaeus* (*T. pygm*), *Trichoniscus pusillus* (*T. pusi*), *Philoscia muscorum* (*P. musc*), *Porcellio scaber* (*P. scab*), *Armadillidium vulgare* (*A. vulg*) and *Ligia oceanica* (*L. oeca*) are from Sutton et al. (1984).

coefficients show a positive correlation between brood weight and fecundity, and a negative correlation between egg size and fecundity (Table 3) in both *L. exotica* and *L. taiwanensis* intraspecifically. Similar results were also found in *A. vulgare* (Lawlor 1976b) and *L. oceanica* (Willows 1987b). Path analysis revealed that higher or lower reproductive allocation is consistently devoted to fecundity (more or fewer eggs) only, with no significant effect on egg size (smaller or larger eggs). The proportion of total fecundity variation that is explained by body size was much more than that correlated with brood size or reciprocal relationships between fecundity and egg size, in both species (Table 4). It seems likely that body size is the dominant correlate with fecundity within both *L. exotica* and *L. taiwanensis*.

A trade-off between number and size of eggs

The most commonly cited reason for egg size not to increase continually is that there is a negative relationship between the number and size of eggs (Roff 1992). Since this assumption was made by Vance (1973a, b) in the studies of the evolution of egg size on planktonic organisms and by Smith and Fretwell (1974) in their pioneering analysis of the evolution of optimal clutch number and propagule size, many analyses have been made for these assumptions of the relationships between clutch size and egg size (e.g., Brockelman 1975, Ware 1977, McGinley et al. 1987, Sargent et al. 1987, Sibly and Monk 1987, Winkler and Wallin

1987, McGinley and Charnov 1988, Sibly et al. 1988). In this study, both species demonstrate a reciprocal relationships between fecundity and egg size. The results suggest that the increment of egg number with body size is in some way limited, and that an increase in egg size would probably cause a reduction in fecundity. Such a correlation may arise because of mechanical constraints (body size, shape, brood capacity, etc.) or ecological or metabolic constraints (limited supply of resources). This trade-off reciprocal relationships between size and number of eggs, seen in both *L. exotica* and in *L. taiwanensis*, seems to match the assumption of the optimality theories of life history evolution (Hutchinson 1951, Cody 1966, Williams 1966, Gadgil and Bossert 1970, Klomp 1970, Schaffer 1974a, b, Sibly and Calow 1983 1985). The concept of trade-off is central to present theories of how life history traits evolve, for it is such trade-offs that limit the scope of variation (Roff 1992).

L. taiwanensis displayed larger relative egg size and smaller reproductive allocation than did *L. exotica*. It seems likely that the reproductive traits of *L. taiwanensis*, such as the smaller reproductive allocation and the heavier eggs (weight-specific), are more in accordance to theoretical predictions of *K*-selected traits rather than those in *L. exotica* (Pianka 1970, Barclay and Gregory 1981, Mueller 1991).

The constraints on evolution of reproductive traits

Berrigan (1991) and Roff (1992) suggested that mechanical factors can potentially influence clutch size in 2 ways: by increasing the load to be carried and hence reducing locomotive ability, or by changing the shape of the organism. In this case, body size is different, while the shape is similar between the 2 species. Fecundity may be constrained by such factors as climbing ability and crevice dwelling. Fig. 3 also shows that fecundity and egg size are a function of body size, which indicates that the size of the isopod is an important factor constraining the size and number of eggs, interspecifically. Sutton et al. (1991) also suggested that egg size and fecundity were constrained by the body size between species.

An intraspecific correlation between egg size and female size has been found in a wide range of taxa, some of which are probably not constrained by mechanical factors especially in some fish and invertebrates (Roff 1992). In this study, the mechanical constraints of body size may be reflected

by a significant positive correlation between egg size and body size. But, in each species only a relatively small part of the egg size variation could be explained by body size (*L. exotica*: 32%; *L. taiwanensis*: 25%) (Table 4). Therefore, other factors such as habitat conditions (e.g., water salinity, humidity, temperature) and food supply, etc., may also be important for achieving optimal egg size, and probably are.

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恆春半島兩種海蟑螂 *Ligia exotica* 及 *L. taiwanensis* 之 生殖特徵的變異

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比較兩種海蟑螂 *Ligia exotica* (Roux) 和 *L. taiwanensis* (Lee) 的生殖特徵。棲息在山溪間的 *L. taiwanensis* 較棲息在海岸潮間區之 *L. exotica* 每單位體重 (weight-specific) 能生產較重的卵 ($F_{1,198} = 166$, $p < 0.001$)；以及較小 ($F_{1,198} = 706$, $p < 0.001$) 的生殖貢獻 (reproductive allocation)。似乎 *L. taiwanensis* 在卵的大小及生殖貢獻兩種生殖特徵上，相對地比 *L. exotica* 合乎理論上 K -選擇的預測 (the predictions for K -selected by the theory)。

當體型大小 (body size) 這個影響生殖特徵的因子以統計的方法移除後，兩種海蟑螂在卵數 (fecundity) 和窩卵重 (brood weight) 之間均存在有顯著地正的相關性；卵數 (fecundity) 和卵重 (egg weight) 之間均存在有顯著地負的相關性；但在卵重 (egg weight) 與窩卵重 (brood weight) 之間則均無相關性。這個結果顯示一種互換 (trade-off) 的關係存在於卵的數目與大小之間，結果似乎合於生活史演化 (life-history evolution) 的最適性理論 (the optimality theories)。

關鍵詞：等腳類，海蟑螂，生殖特徵，生活史演化。

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