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LIFE CYCLE, REPRODUCTIVE PATTERNS AND THEIR YEAR-TO-YEAR VARIATION IN A FIELD POPULATION OF THE WOLF SPIDER *PIRATA PIRATICUS* (ARANEAE, LYCOSIDAE)

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ABSTRACT. Patterns of growth, phenology and reproduction were studied in a field population of the wolf spider *Pirata piraticus* from November 1997 until October 1998 and in June 1999 to unravel the intrapopulation variation and co-variation of these traits. Individuals of *P. piraticus* overwinter as juveniles of different instars while adults were found from the end of April until September. Strong year to year variation in the age and size of overwintering juveniles was present, resulting in a corresponding difference in adult size in the subsequent breeding season. The main period of reproduction occurred from May until August with larger individuals breeding earlier in the season. The size at which adults breed was also significantly different in the successive years. Clutch mass (cocoon mass), clutch volume and fecundity are dependent on the size of the female according to a weakly negative allometric relationship. The differences in those reproductive traits between the succesive years are therefore proportionate to the differences in female size. This was in clear contrast to egg size, a life history trait that shows much less variation and appears to be independent of female size. Therefore, egg size was not significantly different between spring 1998 and spring 1999. There is, however, some variation in fecundity due to egg size and number independent of female size. When corrected for female size, females with larger eggs produce relatively fewer eggs indicating a trade-off between these two reproductive characters.

Keywords: Life history, reproduction, egg size, fecundity, year-to-year variation, *Pirata piraticus*

In wolf spider populations, considerable variation can be observed in phenology (life cycle timing), growth rate, adult size and reproductive output (e.g. Petersen 1950; Edgar 1972; Kessler 1973; Humphreys 1976; Toft 1979; Alderweireldt & Maelfait 1988; Simpson 1993; Maelfait & Hendrickx 1998; Samu et al 1998; Buddle 2000). Most of these studies dealt with only one life history trait and did not look for interrelations between these traits. However, the variation and co-variation of these traits is of particular importance to understand the costs and benefits of a specific life history trait (Stearns 1992; Roff 1992) and can be used to predict changes in life history patterns when environmental conditions change.

In this study we analyzed the life-history of a field population of a common wolf spider *Pirata piraticus* (Clerck 1757) in Belgium. The life-cycle of a field population of this lycosid in Denmark has already been analysed by Toft (1979), who demonstrated that adults of this species appear in spring and females produce one or (possibly) two egg sacs in summer. The hatched juveniles grow during summer and autumn and overwinter as sexually differntiated juveniles or subadults. Juveniles that are born at the end of the summer overwinter a first time as juveniles (not yet sexually differentiated) and a second time during the subsequent winter before they reach the adult stage in May. Laboratory experiments conducted by Schaeffer (1976a, b) revealed that temperature as well as photoperiod are important factors that determine growth and development of this species. Data about intrapopulation size differences, year-to-year variation, and the variation and covariation of adult and reproductive traits are, however, lacking. This information might be of importance to understanding the evolution of the life-history pattern of this species and the interpopulation variation therein.

METHODS

Collection of the animals.—All animals were captured from the same locality, a tidal marsh (Galgenschoor) situated north of the city of Antwerp (Flanders, Belgium) along the tidal river Schelde (51°18′ N, 4°18′ E). The vegetation consisted mainly of common reed (*Phragmithes australis*). Within this tidal marsh, the same area of approximately 10 by 10 m was used as the sampling site. All animals were captured by hand picking. Pitfall traps are useless in these tidal marshes because of the frequent inundations and because pitfall captures have a serious bias caused by differences in activity between the different developmental stages and sexes (Maelfait & Baert 1975; Maelfait 1996). After measuring life history traits of all captured specimens, they were deposited at the Department Biology at Ghent University (Belgium). Sampling was carried out every one or two months from November 1997–October 1998 resulting in a total of 9 sampling occasions, more or less evenly distributed throughout the year. Sampling took place in 1997 on 19 November and in 1998 on 26 February, 1 April, 29 April, 15 May, 17 June, 10 August, 18 September and 21 October. An additional sample was taken 3 June 1999.

Growth and phenology.—For analysis of phenology and growth patterns in the field, only the specimens captured in 1997 and 1998 were used. All animals were kept individually in plastic tubes to avoid cannibalism and the exchange of egg sacs between females. Once transferred to the laboratory, animals were kept in a freezer at −10 °C before measurements were made. All animals were sorted by developmental stage and in the case of adult and larger juvenile spiders also by sex. The criteria to determine a juvenile as a sexually differentiated male was the presence of (slight) swollen palps, while the presence of two (sometimes very small) reddish dots in the central part of the epigastric fold was used to assign an individual as a sexually differentiated female. To determine the size of the animals, the carapace width was measured at its widest point (Hagstrum 1971; Alderweireldt & Maelfait 1988), to the nearest 0.03 mm using a graticule eyepiece fitted to a Wild stereomicroscope

Reproductive traits.—Patterns of reproduction were analysed on females originating from the sampling campaign conducted on 17June 1998 and on females from a second sample, conducted on 3 June 1999 during which only females with an egg sac were collected to study year to year variation in reproductive characteristics. The number of eggs or young present in the egg sac was taken as a measure of fecundity. To obtain a measure of clutch mass, the egg sac (including eggs and/ or juveniles) was weighted to the nearest 0.1 mg on an Ohaus Galaxy 110 electronic balance. The weight of the cocoon itself was negligible compared to its content ($< 0.1\%$).

Before measuring the size of the eggs, they were stored for approximately one month in ethanol 70%. After this treatment, the egg shell becomes fully expanded and size differences between developing and undifferentiated eggs can be neglected. As the shape of the eggs is ellipsoid, egg length as well as egg width was measured to the nearest 0.01 mm. Egg volume was calculated according to the formula: egg volume $= \Pi/6$ x (egg length) $\times$ (egg width)^2.

The product of egg volume and egg number was calculated to obtain a measure of clutch volume. Female mass and, if an egg sac was present, clutch mass, of females captured on 3 June 1999 were additionally weighed to the nearest 0.1 mg on an Ohaus® Galaxy 110 electronic balance.

To correlate reproductive traits with the size of the mother, carapace width was cubed to make it proportional to volumetric measurements like fecundity, clutch volume, clutch mass and egg size.

Data analysis.—Differences in proportions of adult versus juvenile spiders over the different sampling dates were analysed by an R × C independence test (Sokal & Rohlf 1995). To test for size differences between the developmental stages and the different sampling dates, ANOVA was used if assumptions for normality and homogeneity of variance were met. Otherwise, we resorted to non-parametric (Kruskal-Wallis) ANOVA. Multiple comparisons of the different groups were performed with Scheffé test.

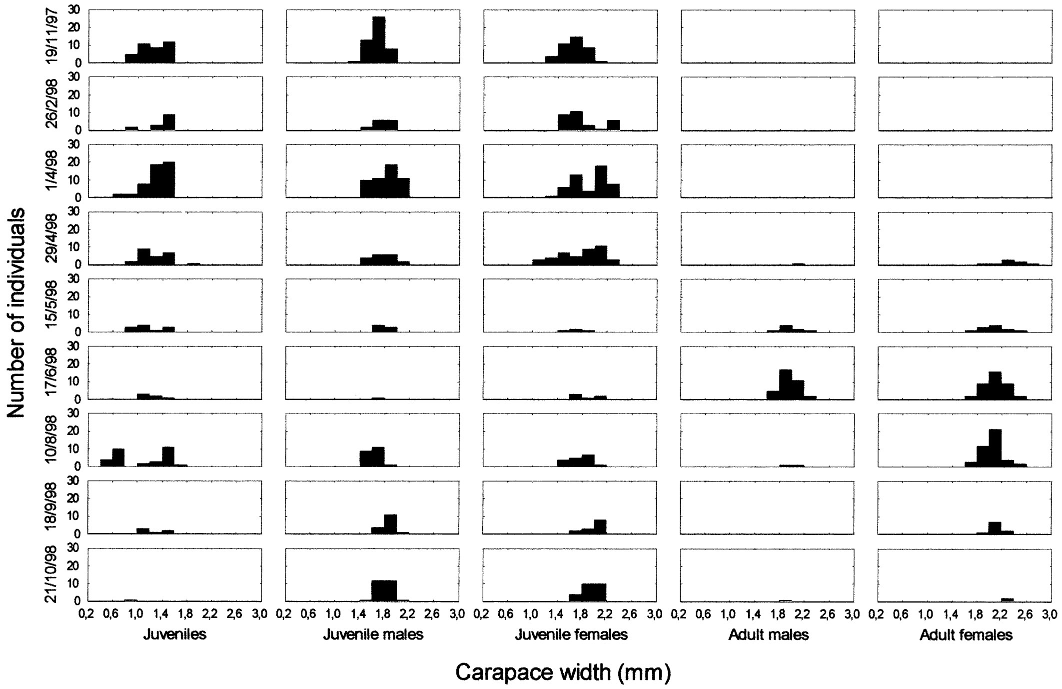

Figure 1.—Frequency distributions of the different developmental stages according to carapace width (mm).

The size distribution of a particular group was analysed by mixture analysis, in which model selection was based on the likelihood ratio test (LR-test). The test was performed by the Mixture 1 program, developed to analyse patterns of fluctuating asymmetry (Van Dongen et al. 1999).

RESULTS

Phenology.—The numbers and the proportions of the different developmental stages over the different samples are depicted graphically on Fig. 1. From November 1997 until the beginning of April 1998, only juvenile spiders were found. From the end of April onwards, adult spiders appear while juvenile spiders were still present. Sexually differentiated males and females were recorded in almost equal numbers over the different sampling dates. The highest proportions of sexually differentiated juveniles were recorded in spring and autumn, while they were almost totally absent in May and June 1998. From November to mid-June, the number of small, sexually undifferentiated spiders present in the samples showed a somewhat similar pattern compared to the number of sexually differentiated juveniles. A high peak in the number of juveniles was observed in August 1998 when juveniles emerged from the egg sac of the adult females. After that a different growth pattern in comparison with the previous year is observed, as small juveniles are already totally absent in October 1998. This difference in proportion of juveniles on October 1998 compared to November 1997 is significant ($\chi^2 = 19.80$; $P < 0.0001$)

Adult spiders emerge from overwintering sexually differentiated and undifferentiated juvenile spiders, as the proportion undifferentiated juveniles encountered during winter differed significantly from the proportion non-adult spiders in May 1998 (29.6% versus 15.2%; $\chi^2 = 0.15$: $P = 0.015$).

The highest proportion of males (40.7%) was recorded on June 1998 and almost all died by August 1998. Females were present until October 1998 with the highest proportions recorded on June 1998 (44.2%) and August 1998 (37.2%).

Growth.—The distrubution of the carapace width of the spiders of the different developmental stages on the different sampling dates

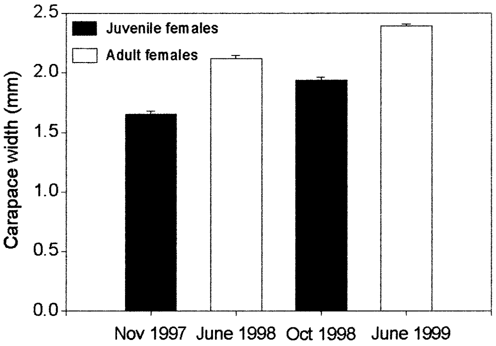

Figure 2.—Carapace width (mm) of juvenile females in their hibernating stage and their adult size in the subsequent spring.

are presented on Fig. 1. A significant bimodality in size distribution is observed in juveniles captured in August 1998 ($LR = 58.77$; d.f. $= 3$; $P < 0.0001$). Juvenile females are on average significantly larger than juvenile males and significantly different over the different sampling dates (two-way ANOVA; sex-effect: $F_{1,\,410} = 5.07$; $P = 0.025$; date effect: $F_{8,\,410} = 10.3$; $P < 0.0001$; interaction: $F_{8,\,410}$; $P = 0.39$). Sexually differentiated juveniles captured in November 1997 are significantly smaller than those captured in April, September and October 1998 ($P < 0.0002$). This implies that sexually differentiated juveniles still increase in size before they reach the adult size.

A comparison of differences in carapace width between males and females could only be performed on adults captured in May, June and August, when a sufficient number of individuals of both sexes were present in the samples. Males have a significantly smaller carapace width than females (ANOVA; $F_{1,\,134}$; $P < 0.0002$). Female size shows a significant heterogeneity over the different sampling dates (ANOVA; $F_{5,\,105}$; $P = 0.003$), with females captured at the end of April being significantly larger than females captured in June and August ($P < 0.05$). Although not significant, the same pattern also appears to exist for males (ANOVA; $F_{2,\,42}$: $P = 0.14$).

The larger overwintering juvenile females in October 1998 compared to November 1997 seems to result in a corresponding increase in size of adult females captured on June 1999 compared to the size of the adult females captured in June 1998 (Fig. 2) (ANOVA; year-effect $F_{1,\,128} = 96.8$; $P < 0.0001$; year x stage affect; $F_{1,\,128} = 0.03$; $P = 0.87$).

Reproduction.—Females with an egg sac were found in May 1998 (60.5%), August 1998 (71.4%) and September 1998 (20.0%). In May 1998, all females had eggs in their egg sac while in August 1998, 18 out of 30 females with an egg sac had first instar juveniles in their egg sac. Female size is not significantly different between females with and females without an egg sac ($F_{1.\,73}$; $P = 0.43$).

As mentioned above, the analysis of the variation and the relationship of reproductive traits and adult female size was conducted on individuals captured in June 1999. There is a great variability for female size measured as carapace width^3 (C.V. = 12.5%); fecundity (C.V. = 17.2%) and clutch volume (C.V. = 17.1%). This is in clear contrast with the variation in egg volume (C.V. = 3.1%), which is very consistent within the population.

The results of the correlation between female size and female mass with the different reproductive traits are presented in Table 1. Clutch mass, clutch volume and fecundity are in all cases positively correlated with carapace width^3. When female mass is taken as a measurement of female size, only clutch mass in the untransformed data, and clutch mass and fecundity in the log transformed data are significantly correlated. No significant relationship is observed between the two measurements of female size and egg size. Higher correlation coefficients are observed between carapace width^3 and the reproductive traits than for female mass and the reproductive traits. A better fit of the data is also observed when both variables are log transformed (higher r-values for all reproductive trait variables). All reproductive traits show negative allometry with female size (slope < 1). However, this is only significant for female mass compared to carapace width^3, indicating that larger females have a relatively lower weight compared to smaller females.

A significant negative correlation between egg size and the residual values of log fecundity on log carapace width^3 ($r = -0.38$; $P = 0.045$) reveales that a trade-off between egg size and fecundity is present (Fig. 3). This negative relationship is not due to the fact that females with larger eggs have a lower clutch volume as shown by the lack of a relationship between egg size and the residual values of

Table 1.—Regression equations between the untransformed and log transformed measurements of female size and some reproductive traits (n = number of individuals). (*) in the log transformed data indicate significant negative allometry (slope < 1; $P < 0.05$).

	n	*r*	*P*	Intercept	Slope
Carapace width^3					
Female mass	28	0.70	<0.0001	7.84	1.36
Cocoon mass	28	0.53	0.004	5.19	0.92
Number of offspring	28	0.40	0.034	18.79	2.51
Egg size	28	0.02	0.937	0.36	0.00
Reproductive output	28	0.45	0.016	5.86	0.96
Female mass					
Cocoon mass	28	0.47	0.011	6.62	0.42
Number of offspring	28	0.33	0.089	25.40	1.05
Egg size	28	−0.10	0.622	0.38	0.00
Reproductive output	28	0.32	0.098	9.77	0.35
Log carapace width^3					
Log female mass	28	0.72	<0.0001	0.61	0.72*
Log cocoon mass	28	0.59	0.001	0.30	0.83
Log number of offspring	28	0.45	0.017	0.80	0.81
Log egg size	28	0.00	0.986	1.14	0.01
Log reproductive output	28	0.48	0.010	0.35	0.81
Log female mass					
Log cocoon mass	28	0.52	0.004	0.17	0.75
Log number of offspring	28	0.38	0.044	0.73	0.70
Log egg size	28	−0.09	0.641	−0.36	−0.06
Log reproductive output	28	0.37	0.051	0.36	0.64

log clutch mass on log carapace width^3 ($r = -0.09$; $P = 0.65$; Fig. 4).

When corrected for female size, no differences between the successive years are noted for fecundity (ANCOVA; $F_{1,\,49} = 0.39$; $P = 0.54$; Fig. 5) and clutch volume (ANCOVA; $F_{1,\,47} = 0.64$; $P = 0.2$; Fig. 6). Slopes of both regressions are not significantly different ($P > 0.56$) . Egg size is also remarkably similar in 1998 and 1999 (ANOVA; $F_{1,\,48} = 0.27$; $P = 0.6$; Fig. 7).

DISCUSSION

The observed life cycle of *Pirata piraticus* for 1998 is in agreement with the patterns observed by Toft (1979). From November 1997

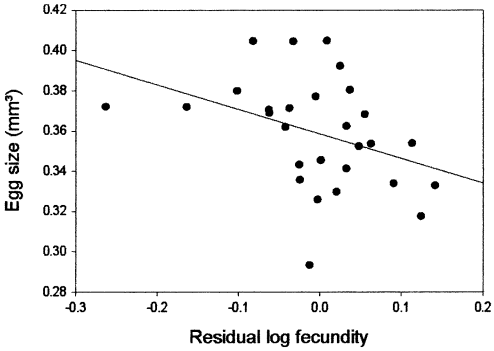

Figure 3.—The relationship between egg size and the residuals of the regression of log fecundity on log female carapace width^3.

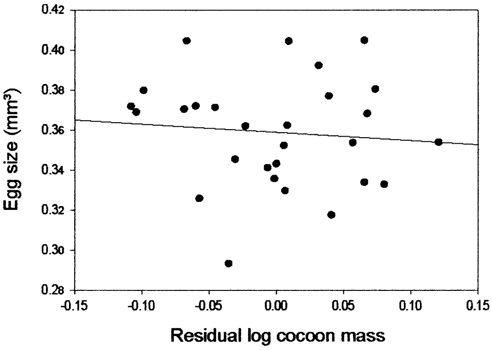

Figure 4.—The relationship between egg size and the residual of the regression of log clutch mass on log female carapace width^3.

until end of April 1998, only juveniles spiders were found. The main period of growth occurs from the second half of June, the period in which the spiderlings emerge until the beginning of the winter period (second half of September). In August, a clear bimodality is observed in the size of the juveniles. This size distribution implies the presence of two different cohorts or time periods at which juvenile spiders are released. As suggested by Toft (1979), it is likely that the group of smaller juveniles originates from a second egg sac produced by the females. The production of a second sac has also been observed frequently in the laboratory (F. Hendrickx, pers. obs.).

Adults that appear early in the breeding season (May) are larger compared to those found in the central period of the breeding season (June–August). As suggested by Alderweireldt & Maelfait (1989), it is likely that these larger individuals overwintered twice before reaching the adult stage.

Perhaps the most striking result is the pronounced difference in size and proportion of juveniles between the successive winters, which demonstrates that growth rate might show strong year-to-year variation. Although to a lesser extent, this year-to-year variation was also observed by Den Hollander (1971) in which ten populations of the *Pardosa pullata* (Clerck 1757) group were studied. Good growth conditions in autumn, possibly due to high temperature or food availability (Schmoller 1970; De Keer & Maelfait 1987; Beck & Connor 1992) might be responsible for the observed differences. It is also important to note that density dependent cannibalism is observed in wolf spiders (Wagner & Wise 1996; Samu et al. 1999) in which larger individuals of the population prey on smaller individuals. Such cannibalism could also be the cause of the absence of small juveniles and the dominance of larger juveniles in autumn of 1998. The larger size of the juveniles in autumn 1998 compared to autumn 1997 is also reflected in the larger adult size in the subsequent spring. This implies that growth conditions in the previous year are largely responsible for the ultimate size of the adults. Beck & Connor (1992) obtained similar results for the crab spiders *Misumenoides formosipes* (Walckenaer 1837). Their study revealed that 90% of the variation in adult size was explained by the variation in final weight of the subadult stage. As all the individuals captured in autumn 1998 in our study were already sexually differentiated, it is likely that all these individuals completed their life cycle in about one year. This means that the adult spiders captured in 1999 were larger than the spiders captured in 1998, although their period of growth was shorter.

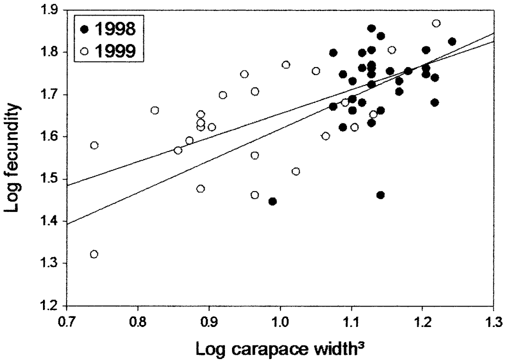

Figure 5.—The relationship between log female carapace width^3 and log fecundity in June 1998 and June 1999.

Concerning the reported interspecific and interpopulation differences in ratio of one- versus two-year old individuals (Schmoller 1969; Den Hollander 1971; Edgar 1972), it is of crucial importance to compare data over several breeding seasons. Edgar (1972) for example recorded interpopulation differences in the proportion of one and two year old individuals in two populations of *Pardosa lugubris* (Walckenaer, 1802). As both populations were sampled in different years, these results have to be interpreted with caution. Additionally, it is not clear whether the two populations contain the same species, as *P. lugubris* comprises a complex of related species (Töpfer-Hoffmann et al. 2000) that have distinct distribution patterns and habitat choices (Hendrickx et al. 2001).

Size of the adult females showed considerable variation within a breeding season with larger individuals breeding earlier in the season. According to the results obtained by Toft (1979) for *P. piraticus* and Alderweireldt & Maelfait (1988) for *Pardosa amentata* (Clerck 1757), it is likely that those larger individuals are descendants of the second egg sac of females that reproduced during summer 1996. The high variability in clutch mass and fecundity is positively correlated with the size of the female. Studies conducted by Kessler

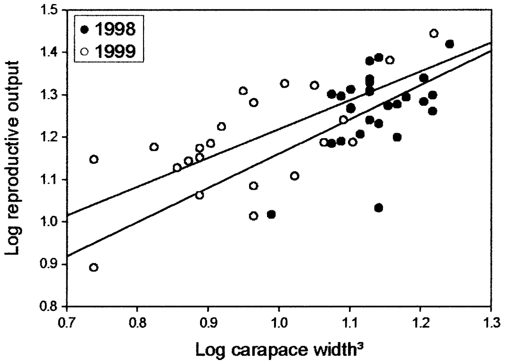

Figure 6.—The relationship between log female carapace width^3 and log reproductive output in June 1998 and June 1999.

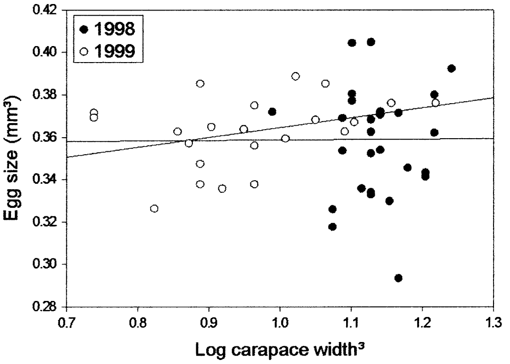

Figure 7.—The relationship between log female carapace width^3 and egg size in June 1998 and June 1999.

(1973), Fritz & Morse (1985) and Kreiter & Wise (2001) revealed that foraging success might be responsible for the additional variation in reproductive succes. As egg size is independent of female size, the observed increase in clutch volume and clutch mass with maternal size is due to an increased fecundity rather then due to an increase in egg size. This is in agreement with the results of other studies conducted on intrapopulation variation in reproductive traits in spiders (Fritz & Morse 1985; Simpson 1993).

When the effect of female size on fecundity was ruled out, a significant negative correlation between fecundity and egg size was observed. Therefore, this additional variation in fecundity due to egg size variation confirms a trade-off between egg size and fecundity (Stearns 1992). Because maternal fitness is the product of offspring number and offspring fitness, maternal fitness is determined by the curve relating offspring fitness to offspring size (Smith & Fretwell 1974; Parker & Begon 1986; Lloyd 1987), which implies that the optimal offspring size a female produces in a particular environment is at the offspring size where an increase in size does not compensate for the related decrease in fecundity and vice versa. The observed lack of correlation between egg size and female size might therefore be expected if offspring fitness is independent of maternal size, as has been observed in a large number of other invertebrates (reviewed in Fox & Csezack 2000).

We found that carapace width^3 is a better predictor for size related reproductive characteristics like fecundity and clutch volume. This is probably due to the fact that that carapace width^3 is a better estimate of female size than female mass is. Carapace width is independent of female condition after egg sac production and therefore a more reliable indicator for female size compared to female mass. Indeed, after the production of the egg sac, females can increase in weight due to feeding; leading to an underestimation of the relative amount of resources devoted to reproduction. Our results also demonstrate that almost all reproductive traits tended to show negative allometry with measurements of reproductive traits. It is important to take this allometry into consideration if a comparison in reproductive traits is made between samples of a different female size (Reist 1986; Roff 1992).

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