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Reproductive allocation in female wolf and nursery-web spiders

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Abstract. We collected data on maternal mass, clutch mass (reproductive effort), number of offspring, and mean offspring mass from 28 species of Lycosidae (wolf spiders) and five species of Pisauridae (nursery-web spiders) found in Mississippi, USA. Our primary goal was to test for a trade-off between offspring number and offspring size (mass) among wolf and nursery-web spiders, which are sister families. The regression of reproductive effort on maternal mass was highly significant and explained 94% of the variation in reproductive effort among species and 96% of the variation among genera. The slope of the regression line between maternal mass and total offspring mass was not significantly different from one, suggesting that spiders used a constant proportion of their total energy budget for reproduction regardless of size. Partial correlation and principal components analyses demonstrated a clear trade-off between offspring size and number. Species with large offspring (relative to adult size) produced fewer offspring than expected. Lycosids produced small numbers of large offspring relative to pisaurids, and smaller species of both families are more constrained in the evolution of the offspring size:number continuum than larger ones.

Keywords: Fitness, life history evolution, offspring size, relative reproductive effort, trade-off

Trade-offs between competing energy demands form the basis of life history evolution because individuals have finite amounts of energy that must be divided into conflicting demands for growth, maintenance, and reproduction (Stearns 1992; Roff 2002; Fischer et al. 2006). The reproductive effort of females must then be further divided: females can invest in producing either larger numbers of smaller offspring or fewer offspring of larger size. Larger offspring are typically considered to be more fit, particularly in harsh environments and when inter- or intraspecific competition strongly limits density (Fox et al. 1997; Fox & Czesak 2000; Olsson et al. 2002; Walker et al. 2003). The relationship between offspring size and fitness, however, can be complex, and there are several notable exceptions to the generalization that larger offspring are more fit (e.g., Sinervo et al. 1992; Gomez 2004). Conversely, there is typically strong selection on female fecundity. All else being equal, fitness increases with increases in the number of offspring produced. Optimal clutch size, producing the greatest number of offspring surviving until sexual maturity, is the result of selection on both adults and offspring (Smith & Fretwell 1974; Fox & Czesak 2000). The number of offspring produced should depend on the shape of the function describing the change in fitness for a given change in offspring size.

Many studies have provided both theoretical (e.g., Smith & Fretwell 1974; Lloyd 1987; van Noordwijk & de Jong 1986; Stearns 1992; Roff 2002) and empirical support for the occurrence of such a trade-off among a wide variety of organisms including copepods, fish, birds, bees, plants, and scorpions (e.g. Stearns 1983; Allan 1984; Smith et al. 1989; Elgar 1990; Kim & Thorp 2001; Leishman 2001; Brown 2003) Although the majority of studies have focused on sexually reproducing species, experimental evidence also exists for similar trade-offs in clonally-reproducing plants (Brewer & Platt 1994; Stuefer et al. 2002). To date, the majority of studies have focused on phenotypic trade-offs between offspring number and size. Recent research, however, has shown a genetic basis for the trade-off in some organisms (Snyder 1991; Csezak and Fox 2003; Mappes and Koskela 2004).

The relationship between female mass, offspring mass, and number of offspring among spider species has been previously examined. In an influential paper, Marshall and Gittleman (1994) reviewed data from the literature to examine the relationship between female body mass and clutch/egg size among a taxonomically broad subset of spiders, but did not find support for a trade-off between egg number and mean egg mass. In contrast, our data were collected totally from wild-caught gravid females, from two closely related families with similar reproductive strategies, and from a small geographic area. The current study focused on wolf spiders (Araneae: Lycosidae) and nursery-web spiders (Araneae: Pisauridae), closely related families in the Lycosoidea (Coddington 2005) to: 1) test for the presence of a trade-off between offspring size and number of offspring, 2) describe patterns of reproductive allocation among females, and 3) report life history data for several species for which little or no information exists.

METHODS

Study animals.—Species within both families exhibit two qualities that make them ideal for this study. Females exhibit similar levels of parental care (but see below), and these species are semelparous. Inclusion of iteroparous species can introduce confounding effects of trade-offs between current and future reproduction and current reproduction and future survival (Desouhant et al. 2005; Waelti and Reyer 2007). During 3 yr of field observations on hundreds of spiders, we have never witnessed multiple clutches in nature for these species in Mississippi. Differing levels of parental care have been shown to influence egg investment (Simpson 1995; Ruber et al. 2004).

Species of both families are found in a variety of habitats and are almost exclusively cursorial hunters. Maternal care in both families can be divided into pre- and post-emergence stages. During the pre-emergence stage, wolf spider females

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Table 1.—Summary of some life history data for wolf spiders (Lycosidae) and nursery-web spiders (Pisauridae). The tabled information includes number of individual spiders sampled from each species (*n*), mean mass of females in mg, mean clutch mass in mg, and the mean number of offspring produced per clutch (Fecundity).

Species	*n*	Maternal mass (mg)	Clutch mass (mg)	Fecundity
Lycosidae				
Allocosa funerea (Hentz 1844)	1	17	13	56
Geolycosa fatifera (Hentz 1842)	2	542	177	118
Geolycosa missouriensis (Banks 1895)	1	742	243	133
Gladicosa pulcra (Keyserling 1877)	10	301	185	164
Hogna annexa (Chamberlin & Ivie 1944)	24	246	160	219
Hogna aspersa (Hentz 1844)	4	1288	694	268
Hogna georgicola (Walckenaer 1837)	59	840	517	236
Hogna lenta A	21	599	418	206
Hogna lenta B	11	642	400	569
Hogna wallacei (Chamberlin & Ivie 1944)	5	544	271	228
Hogna watsoni (Gertsch 1934)	1	140	60	60
Pardosa concinna (Thorell 1877)	7	35	22	60
Pardosa milvina (Hentz 1844)	18	20	19	40
Pardosa pauxilla Montgomery 1904	1	12	7	18
Pirata species A	18	12	7	28
Pirata species B	1	35	27	74
Rabidosa carrana (Bryant 1934)	3	592	341	187
Rabidosa hentzi (Banks 1904)	6	250	149	90
Rabidosa punctulata (Hentz 1844)	340	415	194	143
Rabidosa rabida (Walckenaer 1837)	287	599	373	356
Schizocosa avida (Walckenaer 1837)	11	241	105	212
Schizocosa bilineata (Emerton 1885)	2	66	13	28
Schizocosa duplex (Chamberlin 1925)	5	67	43	76
Schizocosa ocreata grp.	11	70	48	80
Schizocosa saltatrix (Hentz 1844)	17	102	75	116
Schizocosa uetzi Stratton 1997	1	73	37	63
Trochosa acompa (Montgomery 1902)	5	88	71	102
Varacosa avara (Keyserling 1877)	11	96	69	73
Pisauridae				
Dolomedes albineus (Hentz 1845)	3	736	650	668
Dolomedes tenebrosus (Hentz 1844)	1	1947	1540	2627
Dolomedes triton (Walckenaer 1837)	2	642	506	1147
Pisaurina dubia (Hentz 1847)	4	50	40	83
Pisaurina mira (Walckenaer 1837)	21	238	268	348

carry egg sacs suspended from their spinnerets, and nursery-web females carry egg sacs in their chelicerae. The post-emergence stage begins after a period of 4–6 wk for wolf spiders and 2–3 wk for nursery-web spiders, when females must tear open the egg sac in order for spiderlings to emerge. In wolf spiders, once the egg sac has been opened the spiderlings emerge and crawl onto their mother's abdomen where they remain for 1–2 wk before dispersing. Nursery-web females, on the other hand, suspend the opened egg sac from a specially constructed 3-dimensional web structure. Emerging spiderlings crawl onto the nursery web and remain there approximately 1–2 wk before dispersing. During this period, the female does not abandon her offspring but remains close, presumably to defend them (but see Kreiter & Wise 2001).

Measuring fecundity.—We opportunistically collected females carrying egg sacs from throughout Mississippi during March–September 2004, 2005, and 2006. Some gravid females were also captured, but individuals not producing an egg sac within 48 h were not used for the study, to avoid the confounding effects of supplemental laboratory feeding. Most of the species included in this study are nocturnal, and we collected at night using a headlamp to locate eye shine. Several of the wolf spider species have not been previously described and we classified them as morphospecies. Altogether, we collected 28 morphospecies of wolf spiders belonging to the following genera: *Allocosa*, *Geolycosa*, *Gladicosa*, *Hogna*, *Pardosa*, *Pirata*, *Rabidosa*, *Schizocosa*, *Trochosa*, and *Varacosa* and five species of nursery-web spiders in the genera *Dolomedes* and *Pisaurina*. We deposited voucher specimens at the Mississippi Entomological Museum, Mississippi State University, Mississippi State. The number of individuals per species collected was highly variable (mean = 27.7, median = 5, Table 1).

We brought females into the laboratory and maintained them individually in plastic containers measuring 22 × 15 cm. The containers were filled with several cm of commercial topsoil, and dried grass stems were added to provide places for spiders to perch. We kept larger individuals of Pisauridae in 38-l aquaria filled with several cm of commercial topsoil and 2–3 large sheets of pine tree bark provided as a substrate for nursery web construction. We misted containers every other day to provide moisture. Females actually carrying egg sacs did not feed, so that the laboratory diet was not a confounding factor on fecundity. Any burrowing behavior, date of egg sac construction, and date of hatching were recorded at each misting or feeding.

We made the following observations for all wolf spiders. When all spiderlings emerged, we weighed the female and her spiderlings to the nearest milligram. The female was then anesthetized with CO_2 gas and the spiderlings were removed using a soft paint brush. We then weighed the female without the spiderlings and ≥ 30 spiderlings were counted and weighed *en masse*. We collected similar data from nursery-web spiders except that we did not need to anesthetize females or spiderlings. As mentioned earlier, females in this family do not carry emerged offspring but instead create a nursery web eliminating the need for anesthetization to remove offspring. For species producing fewer than 100 spiderlings, all offspring were counted directly. We estimated mean spiderling mass, number of offspring, and total clutch mass using three equations: Total clutch mass = Mass (Female + spiderlings) – Mass (Female); Mean spiderling mass = Total mass of spiderlings counted / Number of spiderlings counted; and Total number of offspring = Total clutch mass/Mean spiderling mass.

Statistical analyses.—We examined the relationships among female body mass and total clutch mass, offspring mass, and number of offspring using least-squares linear regression on natural log-transformed data. The data were transformed in order to prevent one outlier from biasing the regression line and to make the variance in the dependent variable independent of the value of the independent variable (homoscedastic). We also used partial correlation analysis to examine the relationship between offspring mass and number of offspring after removing the effect of maternal body size.

Species data points may not be statistically independent due to traits being shared through common descent; therefore we performed a randomization test using 1,000 permutations to test for a phylogenetic signal. Since the goal of the regression is to look at the variance or invariance of reproductive effort relative to body size, we performed the randomization test on relative reproductive effort. We obtained relative reproductive effort by dividing the total mass of offspring by the mass of the mother (see Reed and Nicholas 2008). We implemented the test using PHYSIGER.M (Blomberg et al. 2003) in MATLAB version 7. We set all branch lengths equal to one, because the topology of the tree for this group is only moderately well known, and estimated branch lengths are unavailable for most species.

To see if the same patterns hold for both taxonomic levels for which we have sufficient replication, all analyses were carried out at both specific and generic levels. As the results were always congruent, regardless of whether species or genera are used, we often provide figures only for the analysis of species.

To determine patterns of reproductive allocation among species and genera we performed principal components analysis (PCA) on the correlation matrix, using varimax rotation. PCA is a multivariate ordination technique appropriate for use in data sets with approximately linear relationships among correlated variables, in this case female mass, offspring mass, and number of offspring. Specifically we were interested in the component that describes explicitly the trade-off between offspring mass and offspring number. PCA analysis was also used to test for differences in reproductive allocation between nursery-web and wolf spiders.

RESULTS

The vast majority of variation in total reproductive energy expenditures can be explained simply by the mass of the mother. Female mass and total clutch mass were positively and highly significantly correlated, with 94% of the variation in total clutch mass explained by female mass at the specific level (i.e., mean value for each species) (F = 519.6, df = 32, P < 0.001, Fig. 1a) and 96% at the level of genera (i.e., mean value for each genus) (F = 222.4, df = 11, P < 0.001, Fig. 1b).

A randomization test performed on relative reproductive effort failed to show a significant phylogenetic signal (P = 0.11). Because of the lack of phylogenetic signal, the narrow taxonomic focus of the study, and a poorly resolved phylogeny of these species, we opted not to perform a phylogenetically-correlated regression analysis.

The slope of the regression line between the natural log of female mass and the natural log of total offspring mass is of particular interest for life history evolution and the evolution of body size, as it relates to the efficiency of energy conversion in similar organisms of varying mass. In the current study, the regression line was not significantly different from one (b = 0.98 ± 0.04 at the specific level and b = 0.92 ± 0.06 at the generic level). This indicates that these species and genera use a constant proportion of their energy for reproduction regardless of body size.

Female mass was also positively correlated with number of offspring and mean offspring mass. Female mass explained 70% of the variation in number of offspring at the specific level (F = 73.4, df = 32, P < 0.0001, Fig. 2) and 69% of the variation in number of offspring at the generic level (F = 22.1, df = 12, P = 0.0008). Female mass explained 59% of the variation in mean offspring mass at the specific level (F = 44.6, P < 0.0001, Fig. 3) and 71% of the variation in mean offspring mass at the generic level (F = 24.7, df = 12, P < 0.001). Like Marshall and Gittleman (1994), we found negative allometry between maternal size and offspring size, so that smaller spiders tend to produce relatively larger offspring. Partial correlation analysis between number of offspring and offspring mean mass showed that number and size of offspring were significantly and negatively correlated at the specific level (r = −0.82) and at the generic level (r = −0.88).

We obtained similar results through principal components analyses. Axis 1 explained 77.6% of the variation among species and is positively correlated with female mass (r = 0.992), offspring mass (r = 0.799), and offspring number (r = 0.841) (Fig. 4). Similarly, the first principal component explained 80.7% of the variation among genera. Axis 1 was highly positively correlated with female mass (r = 0.996), mean offspring mass (r = 0.849), and offspring number (r = 0.842). [In other words, when female mass is included as a variable, the resulting pattern is one of species or genera with larger females having larger offspring and larger numbers of offspring.]

Axis 2 explained 21.5% of the variation among species and is positively correlated with offspring mass (r = 0.597) and negatively correlated with offspring number (r = −0.536). Axis 2 was only very weakly related to female mass (r = −0.027).

The second component explained 18.8% of the variation among genera. Axis 2 is positively correlated with mean offspring mass (r = 0.537) and negatively correlated with

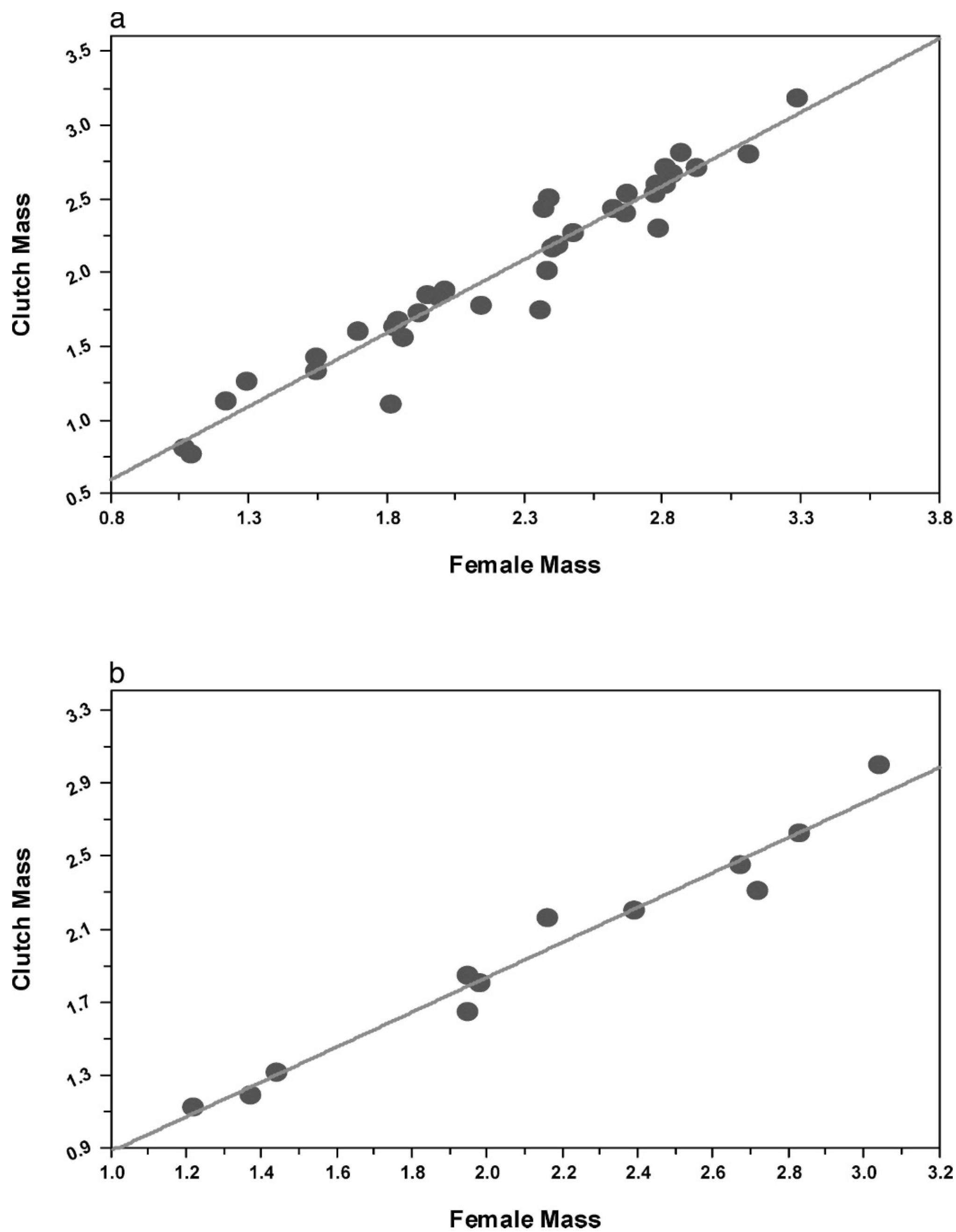

Figure 1.—Least squares linear regression using $\log_{10}$ female mass (in mg) as the independent variable and $\log_{10}$ total offspring mass (in mg) as the dependent variable for *a*) specific means and *b*) generic means. The regressions are highly significant ($P < 0.001$ for both) and explain 94% and 96% of the variation in total clutch mass, respectively.

number of offspring ($r = -0.525$), but shows a very weak relationship to female mass ($r = -0.006$).

Axis 2 was positively correlated with offspring mass and negatively correlated with number of offspring in both of the above analyses. In other words, Axis 2 is reduced into a new variable or component that explicitly describes the inherent trade-off between offspring mass and number of offspring. However, the variation in which we are most interested is reflected in the PCA residuals for offspring mass and PCA residuals for offspring number when regressed against female body size. Both show a high correlation with Axis 2. At the specific level, Axis 2 is positively correlated with residual offspring mass ($r = 0.92$; $P < 0.001$) and negatively correlated with residual offspring number ($r = -0.96$; $P < 0.001$) (Fig. 5). At the generic level, Axis 2 is positively correlated with the residuals from the linear regression of offspring mass onto female mass ($r = 0.93$; $P < 0.001$) and negatively correlated with residuals from the linear regression of offspring number onto female mass ($r = -0.91$; $P < 0.001$). Thus, we feel confident that Axis 2 represents real patterns of reproductive allocation among these species and genera.

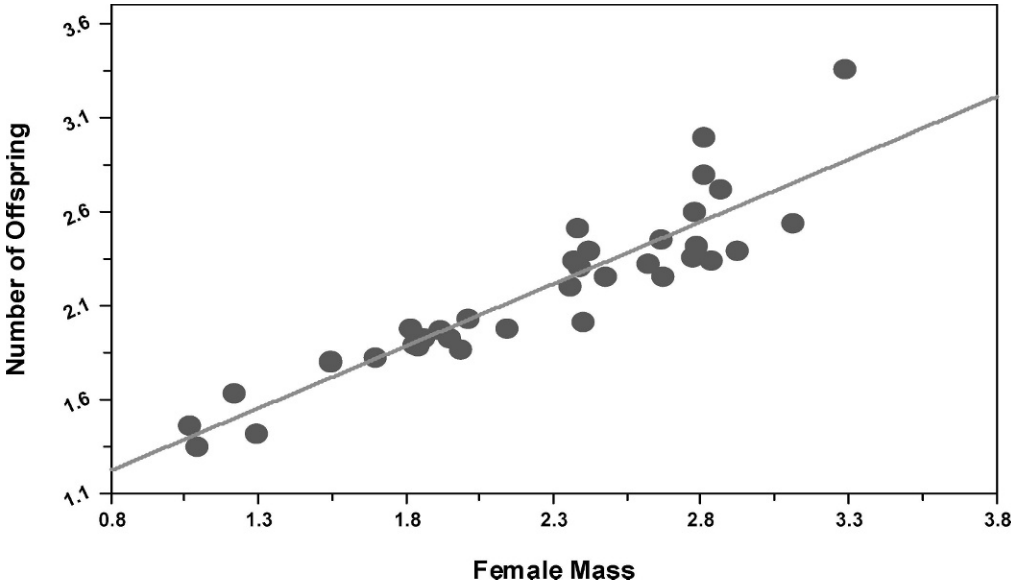

Figure 2.—The relationship between $\log_{10}$ female mass and $\log_{10}$ number of offspring. Female mass explained 70% of the variation in number of offspring at the specific level using least-squares linear regression ($P < 0.0001$).

We also separately regressed Axis 1 against Axis 2 for lycosid and pisaurid spiders (see Fig. 4). The slope for the wolf spiders was negative (-0.52 ± 0.13) and the slope for the nursery-web spiders was positive (0.59 ± 0.34). The two slopes were significantly different from each other (ANCOVA; $F_{2,31} = 4.76$, $P < 0.025$). Thus, lycosids produce smaller numbers of larger offspring relative to pisaurids. Although not statistically testable because of insufficient sample size, there is an obvious bifurcation of the distribution at larger female body sizes for the wolf spiders and nursery web spiders in their allocation patterns. At smaller sizes the two families appear more similar in their allocations patterns.

DISCUSSION

Here we report three major results from our study. 1) Female wolf spiders and female nursery-web spiders have diverged in their reproductive allocation, with wolf spiders generally producing relatively small numbers of large offspring compared to nursery-web spiders. 2) In both families, reproductive effort (total clutch mass) increases in a log-linear fashion with female mass. Larger wolf and nursery-web spiders use neither a larger or smaller portion of their total energy budget for reproduction. 3) In both families, offspring size is negatively correlated with offspring number among species and among genera, indicating a trade-off between

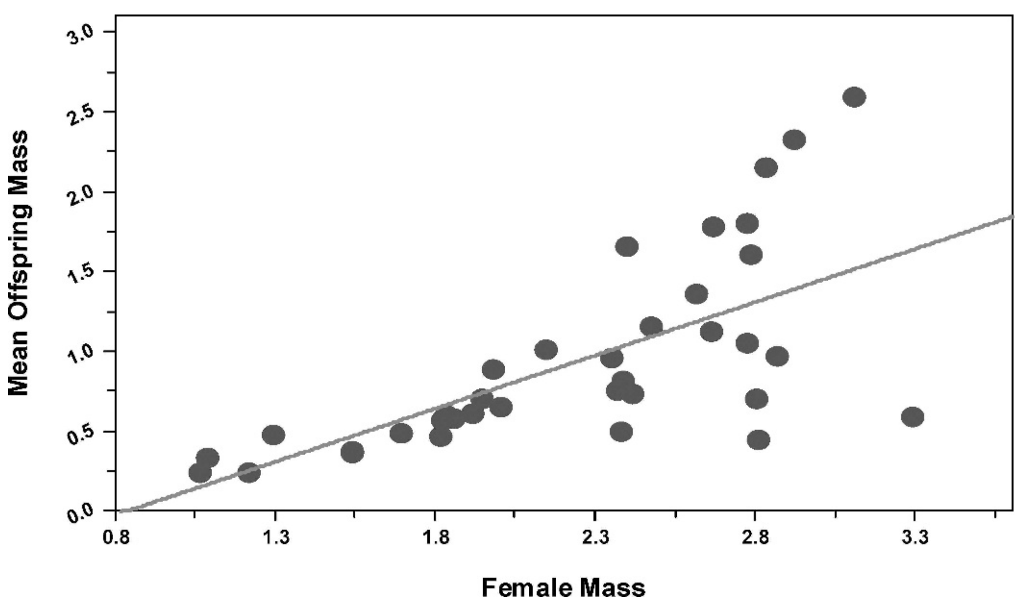

Figure 3.—The relationship between $\log_{10}$ female mass and $\log_{10}$ mean offspring mass. Female mass explained 59% of the variation in mean offspring mass at the specific level ($P < 0.0001$).

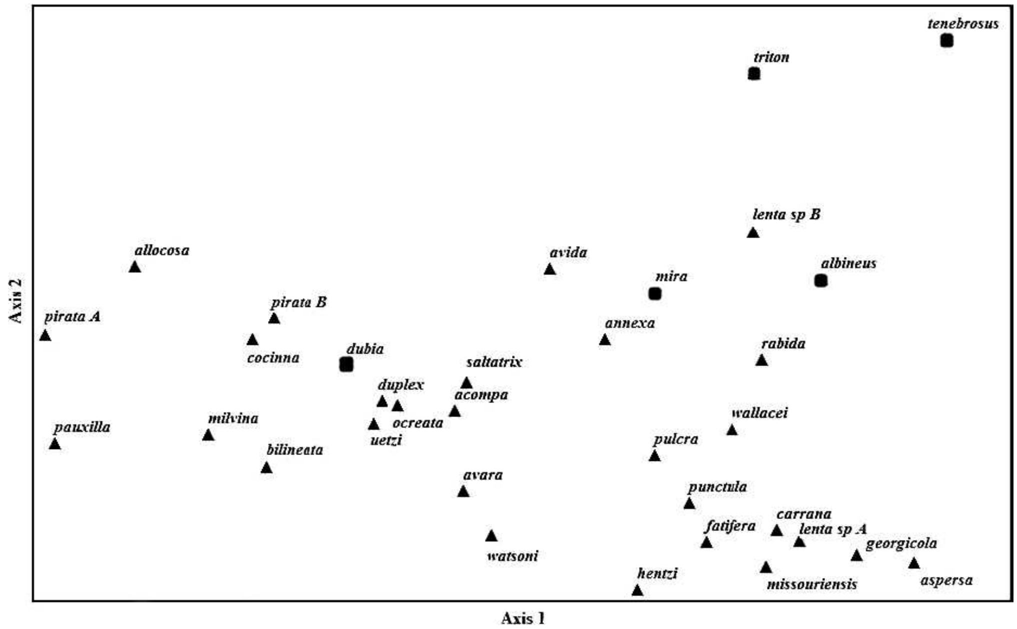

Figure 4.—Principal components analysis demonstrating the trade-off between offspring size and offspring number. Triangles represent species of wolf spider and squares represent species of nursery-web spiders. Axis 1 represents female mass ($r = 0.99$) and Axis 2 is positively associated with number of offspring ($r = 0.60$) and negatively correlated with mean offspring mass ($r = -0.54$). Further, Axis 2 is positively correlated residual offspring mass ($r = 0.92$; $P < 0.001$) and negatively correlated with residual offspring number ($r = -0.96$; $P < 0.001$). Thus, Axis 2 accurately represents patterns of reproductive allocation and demonstrates a trade-off between the two. Noteworthy is the bifurcation of the distribution at larger sizes and the divergence of wolf spiders and nursery web spiders in their allocation patterns.

offspring size and offspring number. Below we provide a brief theoretical background and then elaborate on our findings.

Life history theory predicts a potential trade-off between offspring number and offspring size because there is a finite amount of energy available for reproduction. Thus, all else being equal, selection for larger offspring is predicted to result in a smaller number of offspring (reviewed by Fox and Czesak 2000). Variation in total energy available reflects differences in energy acquisition among different species and among individuals within a species. Differences at the interspecific level may be due to both phylogenetic and environmental influences (Brown 2003). In a seminal paper, van Noordwijk

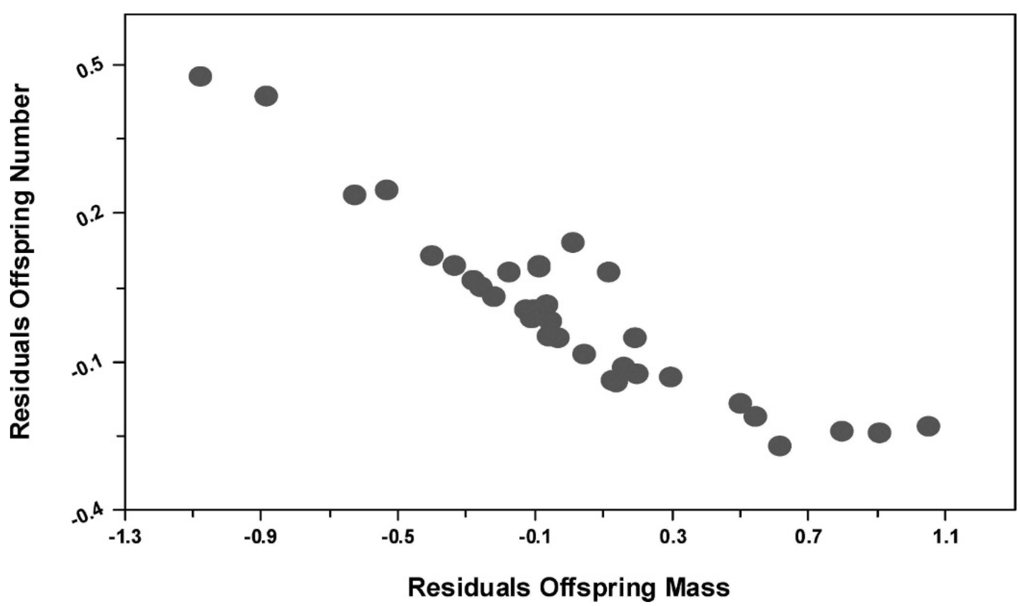

Figure 5.—Residuals from the regressions in Figure 2 and Figure 3 plotted against each other. The regression showed a significant negative relationship between residual offspring mass and residual number of offspring ($r = -0.92$; $P < 0.0001$). The strong negative relations demonstrates a size:number trade-off. Species with larger than average offspring (relative to adult size) also produce fewer offspring that average (relative to adult size).

and de Jong (1986) produced a simple model predicting that when there is variation among individuals in the amount of resources available, the trade-off between individual expenditures will be obscured. Although the van Noordwijk and de Jong model seeks to explain trade-offs at the intraspecific level, the same logic necessarily applies at the interspecific level. Some species will have more energy available for reproduction, on average, than others (i.e., larger species will have more energy). Thus, demonstration of a trade-off in this paper is facilitated by the fact that the species studied use a similar proportion of their available resources for reproduction when averaged across individuals of that species.

Our null hypothesis was that all of the variance in reproductive effort, clutch size, and mean mass of spiderlings could be explained simply by maternal mass. Our data demonstrate that indeed almost all of the variation among the species and genera in total reproductive effort can be explained by mean female mass alone. However, the relationships between female body mass and offspring size or between female body mass and offspring number are considerably more variable. Thus, there exists variation in patterns of reproductive allocation among these species. Our interpretation of the principal components analyses is that most of the variation occurs among the larger species. In particular, the reproductive allocation patterns are quite different between the larger species of pisaurids and lycosids. Pisaurids with large mean female mass tend to produce many small offspring, while similarly-sized lycosids produce fewer, larger offspring. One exception to this pattern is *Hogna lenta B* which has an allocation pattern similar to the pisaurids.

The lack of variation in offspring size among species with small mean female mass suggests some constraint. Female spiders have partially sclerotized reproductive parts, which could constrain resource allocation to a minimum egg size in smaller species regardless of whether the optimal size is a larger clutch of smaller eggs (Foelix 1982). Marshall and Gittleman (1994) found a similar pattern and suggest limits to surface-to-volume ratio of eggs or a minimum size for offspring based on available prey or avoiding desiccation.

Our null hypothesis was that the scaling of maternal mass to clutch mass would be isometric, so that for each incremental increase in size a species would increase its reproductive effort. Indeed, the slope of the regression line between female mass and clutch mass was not significantly different from one. A slope of one suggests a constant relative reproductive effort ($63 \pm 3\%$ of female mass), where larger spiders do not invest a larger or smaller proportion of their available energy than smaller spiders. Our result is consistent with the results of Marshall and Gittleman (1994), who also found a slope of one for a taxonomically broader sampling from the literature. This result is also consistent with results for individuals within species for *Nephila clavipes* (Linnaeus 1767) and *N. pilipes* (Fabricius 1793) (Higgins 1992, 2000, 2002) and also for *Rabidosa punctulata* (Hentz 1844) and *R. rabida* (Walckenaer 1837) (Reed and Nicholas 2008).

Most importantly, we tested for a trade-off between clutch size and offspring size (as per Marshall and Gittleman 1994). We found, among the species of wolf and nursery-web spiders we studied, a strong trade-off between offspring size and number of offspring. This result differs from that of Marshall and Gittleman (1994) who found no such trade-off. Possible reasons for the different conclusion are numerous. Marshall and Gittleman assayed a far broader taxonomic sample than we did, had smaller sample sizes within each species, and included species that are not semelparous. Further, Marshall and Gittleman secured the vast majority of their data from the literature and many of them may have been based on laboratory-reared individuals. For example, *Rabidosa punctulata* is listed by Marshall and Gittleman as producing a mean of 2.5 clutches of eggs. However, four years of mark and recapture data in our Mississippi populations (Reed et al. 2007a,b; Reed and Nicholas 2008) failed to reveal a second egg sac in a wild-caught females of this species. Therefore, the distinct results could be due to greater statistical power present in our less-noisy data set, trade-off being obscured by differences in reproductive behavior (e.g., amount of maternal care), because differences in the broader range of behaviors in the more diverse taxonomic group can confound measures of the amount of energy actually spent on reproduction.

We recommend that future studies on reproductive allocation in spiders focus on large samples of individuals with a narrow taxonomic focus. Most (74%) of the variation in relative reproductive effort was among individuals not among taxonomic groupings in our study. If the trade-off is tested in several well-studied but phenotypically diverse groups of spiders, patterns may become evident concerning what factors influence the presence of the trade-off or might obscure existing trade-offs among behaviorally heterogeneous groups. We also suggest that more data are needed to support or refute the conclusion that the relationship between maternal mass and clutch mass at the species level is the same at diverse taxonomic levels, as suggested here. If such an isometric scaling is shown consistently, theoretical studies might be useful to examine the physiological or evolutionary basis for the constraint.

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