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**Influence of prey size on reproduction among populations of diamond-backed watersnakes
(*Nerodia rhombifer*)**

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Abstract

Average prey size often varies across landscapes, resulting in predator populations having differing access to energetic resources. Shifts in resource quality are likely to cause differences in energy allocation of reproduction. Thus, additional energy intake may lead to: 1) increased offspring size, 2) increased numbers of offspring, 3) increased relative proportion of energy allocated to reproduction, 4) increased absolute amount of energy allocated to reproduction or 5) increased energy allocated to growth of some other no-reproductive function, or 6) some combination of the above outcomes. To test this hypothesis, we evaluated the reproductive allocation patterns of four populations of diamond-backed watersnakes (*Nerodia rhombifer* (Howell, 1852)) that differ in their average prey size. Snakes at large prey sites produced longer, heavier babies compared to snakes from small prey sites. Statistical interactions among sites confounded our ability to compare differences in litter size, litter mass, and relative clutch mass. We suggest that increased prey size results in populations shifting reproductive allocation to increase offspring size. Effects of prey size on litter size, litter mass, and relative clutch mass remain unclear.

Keywords: Life-History, Litter Size, Offspring Size, Relative Clutch Mass, *Nerodia rhombifer*

34 Introduction

35 Life-history theory suggests that optimizing energy allocation to competing functions of
36 the body should maximize fitness within a population (Cody 1966; Gadgil and Bossert 1970).
37 However, the optimal allocation strategy among populations should vary as the prey availability
38 and quality changes (Pianka 1975; Perrin and Sibly 1993; Reznick and Yang 1993; Bronikowski
39 and Arnold 1999). Characterizing the differences in allocation strategies among populations in
40 the field is a major goal in life-history research (Bronikowski and Arnold 1999). Models of
41 optimal allocation patterns in species exhibiting indeterminate growth predict that individuals (or
42 populations) should alter their allocation to reproduction as their energy intake changes
43 (Kozłowski 1996; Heino and Kaitala 1999; Seigel and Ford 2001). Additional energy intake may
44 lead to: 1) increased offspring size, 2) increased numbers of offspring, 3) increased relative
45 proportion of energy allocated to reproduction, 4) increased absolute amount of energy allocated
46 to reproduction or 5) increased energy allocated to growth of some other no-reproductive
47 function, or 6) some combination of the above outcomes.

48 While these predictions make theoretical sense, they are rarely tested in the field.
49 Diamond-backed watersnakes (*Nerodia rhombifer* (Howell, 1852)) occurring in the aquaculture
50 systems of the delta region of Arkansas provide a unique opportunity to study the influence of
51 energy availability on the reproductive allocation strategy among populations. These farms raise
52 different species of fish that vary in size while using similar culturing and pond techniques that
53 minimize extraneous variation among the sites. Differences in the density and size of fish
54 cultured at these sites, as well as the distribution of the size and frequency of consumed prey at
55 each sites, has been previously characterized (Korfel et al. 2015; Chamberlain 2016; and Clifton
56 et al. 2017). Watersnakes occurring on farms producing larger average fish sizes consume larger

average prey. While prey densities among these sites differ, data suggest that farms raising larger fish at lower densities had a similar proportion of adult snakes with prey in their stomachs compared to farms raising small prey at higher densities. Therefore, watersnakes occupying farms with larger prey sizes should have increased energy intake. This system provides a unique opportunity to test the influence of increased energy availability, mediated through access to larger prey, on reproductive allocation (Forsman 1991; Arnold 1993; Forsman 1996; Cundall and Greene 2000; Chamberlain 2016).

Snakes are a fitting model for examining the influence of environmental variation on reproduction because they exhibit variation in offspring and litter traits and they are gape-limited predators (Seigel and Ford 1992; Arnold 1993; Forsman 1996; Forsman and Shine 1997; Bronikowski and Arnold 1999; Bonnet et al. 2000; Shine 2005; Ford and Seigel 2011). Previous studies provide a basis for testing hypotheses concerning the reproductive responses to changing prey characteristics. Although environmental factors can select for shifts in offspring size and litter size, such as over-winter survival, starvation risk or size-specific predator avoidance, prey size should also influence allocation decisions during reproduction (Bonnet 1997; Shine and Downes 1999; Kissner and Weatherhead 2005; Sun et al. 2006).

The goal of this research is to determine if increased environmental energy availability alters the total or proportional energy allocation pattern to reproduction and to explore whether increasing the average prey size available to predators results in increased offspring sizes, litter sizes or both.

Methods

Site descriptions

Four fish farms in near Lonoke, Arkansas were selected for this study, two characterized by large prey and two characterized by small prey. The large prey populations (LARGE) were Joe Hogan State Fish Hatchery (Large1) and Keo Fish Farm Inc. (Large2). Large1 was roughly 105 hectares and produced approximately 80% catfish species (*Ictalurus spp.*). The remainder of production on this farm consisted of crappie and bass species (*Promoxis spp.* and *Micropterus spp.*). The maximum harvest size of catfish and crappie at Large1 was approximately 30 cm, and harvest size of bass is highly variable (Chamberlain 2016; Clifton et al 2017). Large2 was approximately 100 hectares but split between two properties, however only the smaller 40 hectare property was sampled for this study. This site specialized in the production of hybrid striped bass (*Morone saxatilis* (Walbaum, 1792) / *Morone chrysops* (Rafinesque, 1820)) and triploid grass carp (*Ctenopharyngodon idella* (Valenciennes, 1844)), with 50% of property dedicated to each fish species. The maximum harvest size for grass carp and hybrid striped bass at Large2 was 25 cm (Chamberlain 2016; Clifton et al 2017). The two small prey sites (SMALL) were Gentry and Canterbury Fisheries LLC (Small1) and Pool Fisheries Inc. (Small2). Both sites specialized in the production of fathead minnows (*Pimephales promelas* (Rafinesque, 1820)) and goldfish (*Carassius auratus* L., 1758). However, snakes at these sites only had access to the goldfish, which are harvested at a maximum size of 7.5 cm (Chamberlain 2016; Clifton et al 2017). Small1 was approximately 65 hectares and Small2 was approximately 135 hectares in size. A more complete summary of prey characteristics at all four sites can be found elsewhere (Korfel et al. 2015; Chamberlain 2016; Clifton et al. 2017,).

We chose these sites because of their close proximity and environmental similarity. All sites consisted of series of rearing ponds ranging from 0.1-0.8 hectares with maximum depths of 3 m and exposed, grassy banks. All sites hosted avian and mammalian predators, such as great

blue herons (*Ardea herodias* L., 1758), great egrets (*Ardea alba* L. 1758), American mink (*Neovison vison* (Schreber, 1777)), and striped skunks (*Mephitis mephitis* (Schreber, 1776)). Additionally, hybrid striped bass and catfish farmed at the LARGE populations were likely aquatic predators of neonate snakes. The maximum distance between any two sites was 15 km. However, due to lack of suitable habitat between sites, gene flow among sites was assumed to be limited.

Study Animals:

Pregnant snakes were hand-captured in late summers of 2012-2014 at all sites (total=124; 33, 33, 29, 29 from Large1, Large2, Small1, and Small2 respectively). Snakes were brought back to the laboratory and housed individually in size-appropriate plastic cages within a rack system. They were provided a thermal gradient of 23-32°C via thermal heating elements placed under the rear third of each cage (Vision Products, Canoga Park, CA). All snakes were provided aspen bedding, water, and fed once weekly *ad libitum* on size-appropriate goldfish. Time spent in captivity did not significantly differ among sites nested within prey type (PREY: $F_{1,110} = 0.0040$, $P = 0.9495$, PREY:SITE: $F_{1,2} = 1.9956$, $P = 0.1408$). Further, a mother's time spent in captivity is expected to have little effect on reproductive output as placental transport of organic molecules is minimal for diamond-backed watersnakes since this species is highly lecithotrophic (Stewart and Castillo 1984). The mean and standard deviation of days in captivity were 42 ± 25 , 44 ± 26 , 49 ± 17 , and 38 ± 16 for Large1, Large2, Small1, and Small2 respectively. Dam snout-vent length (SVL) and body mass were measured at the time of capture, henceforth called pre-parturient mass. Upon parturition, dam body mass was re-measured, henceforth called post-parturient mass. A total of 2,149 offspring were measured (621, 609, 411, 508 from Large1, Large2, Small1, and Small2 respectively). Litter size (live only), litter mass (live only), and each

126 offspring SVL and body mass were recorded. All dams and offspring were individually marked
127 and released to their native population within a week of birth. Animals were cared for in
128 accordance with guidelines the *Guide for the Care and Use of Laboratory Animals* (1996,
129 published by National Academy Press, 2101 Constitution Ave. NW, Washington, DC 20055,
130 USA). This project was covered under Institutional Animal Care protocol R-12-03 and Arkansas
131 Game and Fish permit #031220131.

132 **Statistical Analysis:**

133 To test whether females from populations with access to differing sized prey allocate a
134 different proportion of their total energy to reproduction, we propose the use of relative clutch
135 mass ($RCM = \text{litter mass} / (\text{litter mass} + \text{post-parturient mass})$), a measure of the relative
136 proportion of female's total mass that is comprised of reproductive material (Seigel et al. 1986).
137 Conceptually, this measure allows comparison of reproductive investment among individuals of
138 the same species. To test if increased absolute amount of energy allocated to reproduction there
139 should be an increase in average offspring size, litter size, or both among females from each site.
140 Lastly, if additional energy is not being allocated to reproduction, then females should not differ
141 in any of the measured reproductive traits.

142 Data were analyzed in the R platform (R Core Team, 2014). All analyses on offspring
143 mass and offspring SVL were performed using either a mean value for each litter. Data were
144 tested for normality to meet the assumptions of parametric testing. Data were either natural log-
145 transformed or square-root transformed to meet assumptions of normality where necessary. All
146 data were analyzed using a nested design, with sites nested within prey type.

147 Because dam body-size is known to correlate with most reproductive characteristics in
148 other snake species, analyses of covariance (ANCOVA) were used to measure population

differences in reproductive traits with dam SVL as a covariate (reviewed in Ford and Seigel 2011). We performed analysis of variance (ANOVA) and ordinary least squares regression if dam SVL did not correlate with a particular reproductive trait. ANCOVA models with significant interaction terms of dam SVL to factor terms were not interpreted, as they fail to meet the assumptions of common slopes. Non-significant interaction terms were removed from all models and only reported when their $p < 0.10$. When data were missing for a given trait, each litter with missing data was removed from the analysis. Statistical significance was determined at $\alpha < 0.05$. Significant ANCOVA, ANOVA, and linear models were further analyzed to detect population differences using post-hoc analyses with a Tukey correction.

Results

Offspring size:

Mean natural log-transformed offspring mass significantly increased with female SVL and differed by prey type, with no interaction of PREY on SVL and effect of SITE nested within PREY was insignificant (SVL: $r^2 = 0.338$, $F_{1,116} = 32.152$, $P < 0.0001$; PREY: $F_{1,116} = 25.929$, $P < 0.0001$; SVL*PREY: $F_{1,116} = 0.4213$, $P = 0.51276$; PREY:SITE: $F_{1,2} = 1.2865$, $P = 0.2803$, Fig. 1a). Snakes from LARGE sites produced heavier babies than snakes from SMALL sites ($t = -4.828$, $P < 0.0001$). Mean offspring mass was 23% larger at LARGE sites than at SMALL sites (LARGE = 10.5 ± 0.2 g; SMALL = 8.5 ± 0.2 g, mean $\pm$ s.e.).

Mean offspring SVL also significantly increased with female SVL and differed by prey type, with no interaction of PREY on SVL and effect of SITE nested within PREY was insignificant (SVL: $r^2 = 0.235$, $F_{1,116} = 19.696$, $P < 0.0001$; PREY: $F_{1,116} = 14.444$, $P = 0.0002$, SVL*PREY: $F_{1,116} = 0.0692$, $P = 0.7929$; PREY:SITE: $F_{1,2} = 0.4484$, $P = 0.6398$, Fig. 1b).

Snakes from LARGE sites produced longer babies than snakes from SMALL sites ($t = -3.392$, $P = 0.0010$). Mean offspring length was 4.5% longer at LARGE sites than at SMALL sites (LARGE = 25.2 ± 0.2 cm; SMALL = 24.1 ± 0.1 cm, mean $\pm$ s.e.).

Litter size:

Litter size was square-root transformed to meet the assumption of normality. Litter size strongly increased with female SVL ($r^2 = 0.3882$, $F_{1,111} = 66.878$, $P < 0.0001$); however, SITE nested within PREY was significant and an interaction between SVL and SITE nested within PREY was significant within the full model and made interpretations impossible as the assumption of the homogeneity of regression slopes was violated (PREY:SITE: $F_{1,2} = 3.4962$, $P = 0.03388$; SVL*PREY:SITE: $F_{1,111} = 4.2301$, $P = 0.01701$). The interaction of SVL with SITE nested within PREY suggested that litter size did not scale with SVL similarly among sites. This can be more easily understood by visualizing the nature of these relationships by SITE instead of PREY (Fig. 2a). It was clear from this analysis that the relationship of litter size to female SVL for snakes at Small1 had a substantially shallower slope than at Small2; whereas, both LARGE sites had similar relationships of female SVL to litter size.

Litter mass:

Natural log-transformed litter mass significantly increased with female SVL; however, the significant interaction between SVL with SITE nested within PREY made interpretation impossible as the assumption of the homogeneity of regression slopes was violated (SVL: $r^2 = 0.376$, $F_{1,111} = 58.326$, $P < 0.0001$; PREY:SITE: $F_{1,2} = 2.8137$, $P = 0.0609$; SVL*PREY:SITE: $F_{2,111} = 2.8978$, $P = 0.05952$). Similarly, visualizing this interaction in terms of SITE instead of PREY helped to decipher patterns (Fig. 2b). Again, the relationship of litter mass to female SVL at Small1 had a substantially shallower slope than the other SMALL site, as well as both LARGE sites.

198 Relative clutch mass:

199
200 Relative clutch mass significantly correlated with female SVL; however, SITE nested
201 with PREY was significant and an interaction between female SVL and SITE nested within
202 PREY was significant within the full model and made interpretations impossible because the
203 assumption of the homogeneity of regression slopes was violated (SVL: $r^2 = 0.1625$, $F_{1,111} =$
204 5.5961 , $P = 0.01982$; PREY:SITE: $F_{1,2} = 2.9991$, $P = 0.05408$; SVL*PREY:SITE: $F_{1,108} = 3.001$,
205 $P = 0.01404$). Again, visualizing by SITE rather than PREY, as with litter size and litter mass,
206 helped clarify this relationship (Fig. 2c). Relative clutch mass scaled negatively with SVL at
207 Small1, whereas it scaled positively at Small2.

208 A consistent pattern was evident in the relationships of litter size, litter mass, and relative
209 clutch mass to maternal SVL; the regressions for Small1 scaled with shallower slopes than those
210 regressions from the corresponding than for Small2. Meanwhile, both LARGE sites behaved
211 similarly when comparing their slopes of litter size, litter mass, and RCM to female SVL. In an
212 effort to explain the SMALL site pattern in the scaling of each reproductive trait to female SVL,
213 we tested whether they differed in variability of these traits. We specifically tested whether
214 shallower slopes at Small1 were associated with increased variation in these traits for larger
215 females as compared to Small2. We calculated the absolute value of the residuals of each
216 reproductive trait regressed on female SVL for both populations and tested for a correlation
217 between these residuals and female SVL for the three reproductive traits separately. Absolute
218 values of residuals were used as we were strictly interested in measuring the absolute deviation
219 from the regression line and not whether these values were above or below the regression line,
220 thus avoiding the effect of regression towards the mean. Therefore, if a positive correlation exists
221 at a site between SVL and absolute value of residuals of a particular reproductive trait regressed

on female SVL, then the deviations from the mean regression line increases with female body size.

The relationship between variation in litter size and female SVL differed between Small2 and Small1; Small1 exhibited a positive slope compared to Small2, which had a slope that did not differ from zero (SVL: $F_{1,53} = 9.196$, $P = 0.0037$; SVL*SITE: $F_{1,53} = 7.666$, $P = 0.0077$, Fig. 3a). This suggested that at larger SVL's females from Small1 produced litters that varied more in size than did females from Small2. Similar relationships occurred for litter mass and RCM; Small1 snakes had larger absolute residuals at longer SVL's compared to snakes from Small2 (litter mass, SVL: $F_{1,53} = 4.251$, $P = 0.0442$; SVL*SITE: $F_{1,53} = 9.980$, $P = 0.0026$; RCM, SVL: $F_{1,53} = 3.981$, $P = 0.0512$; SVL*SITE: $F_{1,53} = 9.789$, $P = 0.0029$). These results suggest increased variation in litter mass and RCM at larger body sizes at Small1, which resulted in a steeper positive slope for these relationships compared to individuals from Small2 (Figs. 3b and 3c).

Discussion

Here we present evidence that prey size variation can have a profound influence on reproductive allocation patterns in diamond-backed watersnakes. Snakes feeding on larger prey had longer and heavier babies compared to similarly-sized snakes from sites that had access only to small prey (Figs. 1a and 1b). The influence of prey size on litter size, litter mass, and relative clutch mass is less clear because of significant interactions suggesting that, for these traits, factors of prey type and sites within prey type did not scale similarly with female SVL (Figs. 2a-c). Post-hoc examination suggests these interactions are likely due to a high degree of variation in reproductive traits in snakes with longer body sizes at Small1, which resulted in a similar shallow slope in the three regressions of litter size, litter mass, and RCM on female SVL (Figs.

3a-c). The increase in offspring size at LARGE sites and lack of clear pattern in differences of litter size between SMALL and LARGE sites provide provide marginal support for an increase in total energy allocation to reproduction at LARGE sites. We are unable to determine if prey size changes influence the relative proportion energy allocated to reproduction because of the inability to resolve patterns of RCM between SMALL and LARGE sites.

The strongest effect of increasing prey size was a dramatic increase in mass and length of offspring. While size-specific predation, starvation risk, and overwinter survival (Bonnet 1997; Shine and Downes 1999; Kissner and Weatherhead 2005; Sun et al. 2006) favor larger offspring size and could be influencing these sites, it is likely that snakes occupying all fish farms experience these environmental variables to a similar degree. We therefore conclude that the major selective force on offspring size in these populations is driven by differences in prey size.

Previous work has shown that average adult body size within a population is selectively driven by differences among populations in average prey size. Snakes colonizing islands with average prey sizes larger or smaller than the ancestral mainland population, for example, often result in gigantism or dwarfism (Forsman 1991; Boback 2003; Keogh et al. 2005; Aubret and Shine 2007). Unfortunately, these studies typically examine prey size effects on adult body size and do not consider the effect of prey size on reproductive allocation or the response of offspring to increasing the average prey size. However, we are not the first to document that prey size can result in increasing mean offspring size in snakes. Sun et al. (2006) showed that average size of offspring in insular vipers was larger than mainland counterparts. These authors argued that the increase in offspring size was due to the need for neonatal vipers to quickly attain sizes that allow them to forage on proportional large birds that stopover during migration on their study island. Gape-limitation produces a strong selective pressure for increased SVL size of neonates.

268 Mainland vipers, in contrast, feed on diverse prey with variable body sizes and produce offspring
269 that are less than half the length of offspring from the insular population.

270 Thus, larger offspring may be an indirect effect of prey size. The ability to eat large prey
271 is limited by gape elements of the skull in macrostomatan snakes (Cundall and Greene 2000).
272 Longer gape elements increase the ability of macrostomatan snakes to swallow larger prey by
273 aiding in the biomechanics of handling and swallowing prey (Cundall and Greene 2000; Vincent
274 et al. 2006). If cranial gape elements are unable to respond to selection of larger prey
275 independently, selection for an overall larger body size would achieve the same results as a
276 function of positive allometries.

277 The selective force of prey size may operate at multiple levels in ontogeny to increase
278 offspring size. If small prey are rare or unavailable at birth due to timing of life-histories of the
279 prey or, in our case, because of anthropogenic interference associated with culturing fish-stock,
280 selection should favor increasing neonate size to a point where neonates can begin to
281 immediately forage. If prey is still too large at the time of birth, then increasing offspring mass
282 could fuel post-natal growth from energetic reserves until neonates are large enough to begin
283 foraging on available prey (Madsen and Shine 2002; Sun et al. 2006). Even if small prey are
284 available to neonates, selection may still favor longer or heavier offspring if larger, more
285 energetically-rich prey are available but un-attainable due to their size (Sun et al. 2006).
286 Increasing both initial offspring mass and length should shorten the growth time necessary for
287 neonates to access these more favorable prey.

288 Either or both of these explanations may be operating among our sites to drive
289 differences in offspring size. While both LARGE sites stock small fish fry between April and
290 July, small prey at the time of birth of neonate snakes in August to October are rare as only those

fish stocked in June or July will not have grown beyond what neonate snakes can physically handle. Because of this time-delay of stocking, differential feeding of fish among ponds, and the retention of larger size classes of fish awaiting sale and shipment, larger and more calorically-valuable prey are always more abundant. Thus larger neonates at LARGE prey sites have access to more prey both immediately and through ontogeny. To further support this argument, observations of snake diet through ontogeny, including that of *N. rhombifer*, show that as snakes grow larger, individuals (particularly females) preferentially drop smaller prey items from their diet (reviewed in Arnold 1993, but see also Mushinsky et al. 1982, Plummer and Goy 1982).

The advantage of larger offspring to access larger prey is greatly diminished at SMALL sites because these sites have abundant small prey on which neonates can immediately begin foraging. But, there are still larger prey available, which might offer an energetic advantage, suggesting a benefit to starting life at a larger size. However, two factors may diminish this advantage compared to LARGE sites. First, the maximal prey size at SMALL sites is smaller, meaning that intermediate-sized snakes quickly lose a size advantage, and large snakes are likely to be constrained by needing to feed on relatively small prey. Slowing the rate at which larger body sizes are reached may be advantageous, which could be achieved by beginning as a smaller neonate. Secondly, the largest prey sizes at SMALL sites are rarer than smaller prey sizes due to commercial demand.

We were unable to interpret of the effect of prey size on litter size, litter mass, and RCM initially due to the increased variation in these traits at Small1. Why did variation in litter size, litter mass, and RCM increase with body length at this site and not the other SMALL site, Small2? We have identified two potential explanations that may address this discrepancy. 1) While these sites raise the same fish species to approximately the same sizes, they might not

raise them at the same frequency. If Small1 does not use all of its rearing capacity, either by not stocking as many ponds at one time or by not stocking at the same level throughout the year, prey may become more patchily distributed and harder to acquire for pregnant females. 2) Even if sites have the same size fish, raised at the same frequencies, these sizes may not be available in the same proportions. Small1 might raise the largest-sized fish at a lower proportion of its total. This would require large females to either begin foraging on smaller prey more often, or move more frequently to find ponds with large prey.

In either explanation, larger females that need more fuel to supply greater reproductive demands (since reproductive output is correlated with body size) will suffer a greater cost than smaller females when large prey become scarce. Both mechanisms would result in some large females successfully foraging while others would fail to locate appropriate food resources. Consequently, some large females will be able to fuel reproduction while others will not, leading to increased variation in reproductive output as female body size increases (van Noordwijk and de Jong 1986). In a similar scenario between two populations of checkered gartersnakes (*Thamnophis marcianus*), Seigel and Ford (2001) found that populations differed in phenotypically plastic response of reproductive traits in response to prey availability. A population with access to constant prey showed little variation in reproduction, which they suggest is a response to the lack of selective pressure to respond to variation in prey availability. However, a population with dramatic seasonal variation in prey availability showed substantial variation in reproductive traits in response to sudden bursts of prey of high food availability. Similar selective pressures could push Small1, but not Small2 to exhibit similar plasticity in reproductive traits.

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345

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429 Figs. 1 a-b. LARGE and SMALL sites significantly differ in both mass (a) and length (b) of
430 offspring correcting for the effect of maternal body-size. Female watersnakes at LARGE sites
431 produce offspring that are both heavier and longer than offspring from SMALL sites. There is no
432 significant interaction between female SVL and either offspring mass or SVL. LARGE prey sites
433 are represented by (●) and SMALL prey sites by (○).

434
435 Figs. 2 a-c. Strong interactions of female body length and site exist for litter size (a), litter mass
436 (b), and relative clutch mass (c). In all three panels, Small1 consistently behaves differently than
437 its corresponding SMALL site Small2, while both LARGE sites behave similarly for all three
438 traits. This suggests that the significance of these interactions may be driven by Small1. LARGE
439 sites are represented by filled symbols: Large1 (●) and Large2 (▲). SMALL sites are represented
440 by unfilled symbols: Small1 (○), Small2 (Δ). Regression line of Large1 is represented by (—),
441 Large2 by a (---), Small1 (· - ·), and Small2 by a (···).

442
443 Figs. 3 a-c. Variation in the absolute value of residuals of litter size to female body size (a),
444 absolute value of residuals of litter mass to female body size (b), and the absolute value of relative
445 clutch mass to female body size (c) all increase with female body length at Small1, represented
446 by a (○), resulting in a positive correlation. Small2 residuals, represented by a (Δ), do not
447 correlate with female body length, resulting in near flat slopes.

448

79x34mm (300 x 300 DPI)

158x137mm (300 x 300 DPI)

158x137mm (300 x 300 DPI)