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Generality of the Terminal Investment Hypothesis: Effects of Extrinsic Mortality and Resource Availability on Age-Related Reproductive Investment

Allystair Dunngannon Jones

A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Master of Science

Mark C. Belk, Chair
Jerald Johnson
G. Bruce Schaalje

Department of Biology

Brigham Young University

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ABSTRACT

Generality of the Terminal Investment Hypothesis: Effects of Extrinsic Mortality and Resource Availability on Age-Related Reproductive Investment

Allystair Dunngannon Jones
Department of Biology, BYU
Master of Science

A central question in life history theory is, what combination of traits and behaviors will lead to the highest reproductive success throughout a lifetime. The trade-off between current and future reproduction is central to the lifetime reproductive success of an organism. If there is a cost to reproduction, then allocation of energy to current reproduction will come at a cost to future reproduction. We expect young individuals to favor future reproduction over current reproduction and that balance shifts to current reproduction as they age (i.e. terminal investment hypothesis). However, how this transition from an emphasis on future reproduction to emphasis on current reproduction changes throughout a lifetime should depend on environmental factors like mortality and resource availability. We test for the generality of terminal investment across three species of poecilliid fishes in a range of environments. We found evidence of terminal investment in all three species in both high and low mortality environments and high and low resource availability environments. In general, high mortality or high resource availability tended to result in a decreased slope of the relationship between reproductive allocation and body size. Terminal investment appears to be general, even though there was an effect of high mortality and resource availability, it was not sufficient to completely preclude terminal investment.

Keywords: life history, terminal investment, cost of reproduction, Poeciliidae, reproductive investment

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Introduction

A central question in life history theory is, how do organisms allocate energy over their lifetime among the competing processes of growth, maintenance, and reproduction to maximize their evolutionary fitness (Fisher 1930, Williams 1966, Stearns 1977, Roff 1992)? Allocation of energy among these competing demands generates tradeoffs because time and energy allocated to one of the competing processes will reduce the time and energy available for other processes. A key life history trait is the trade-off between current and future reproduction (Williams 1969, Stearns 1992, Harshman and Zera 2007, Speakman 2008). A prevalent hypothesis that predicts how organisms might balance this trade-off is the terminal investment hypothesis (Clutton-Brock 1984). According to this hypothesis, young individuals should allocate more energy to future reproduction relative to current reproduction, but as individuals age, the balance between current and future reproduction should shift increasingly to current reproduction. In organisms with indeterminate growth, this creates a hyper-allometric pattern of reproductive measures compared to body size because allocation to reproduction would increase with age at a faster rate than body size (Curio 1983, Clutton-Brock 1984, Roff 1992, Stearns 1992, Forslund and Pärt 1995).

Several studies have addressed the terminal investment hypothesis (Reid 1988, Part 1992, Poizat 1999, Billing 2007, Belk and Creighton 2011), however, few researchers have examined whether terminal investment patterns vary across environmental gradients that might affect the trade-off between current and future reproduction (i.e., the generality of the terminal investment response). One such gradient is extrinsic mortality rates (Reznick and Endler 1982, Johnson and Zuniga-Vega 2009). For example, predator-mediated mortality has been shown to be a potent force in life history evolution (Reznick and Endler 1982, Johnson and Belk 1999, 2001, Johansen 2004, Hilton et al. 2010). High predation pressure on juveniles favors rapid growth through the

juvenile phase, as well as maturation at larger size and delayed maturity (Reznick and Endler 1982). When adults experience high predation pressure, selection favors reduced age and size at maturity and increased early allocation to reproduction (Shaffer 1974, Law 1979, Michod 1979). What has not been well studied is how changes in mortality affect the within-lifetime pattern of reproductive allocation such as terminal investment.

Another environmental gradient that can affect life history evolution is resource availability (Boekelheide and Ainley 1989, Syderman et al. 1991, Roff 1992, Stearns 1992, Pons and Migot 1995). Reproductive investment is a function of available resources and effects of investment on future survival (Roff 1992, Stearns 1992). The optimal level of reproductive investment can be influenced by resource type (McGinley and Charnov 1988), resource availability during provisioning (Lloyd 1987, McGinley et al., 1987) and resource predictability (Lalonde 1991). Low resource availability selects for delayed maturity, reproduction at smaller size, and reproduction later in life (Tinkle and Collins 1974, Wilbur 1974, Winemiller 1993). In contrast, high levels of resource availability will select for increased growth rates, larger body size, and reproduction earlier in life (Hirshfield and Tinkle 1975, Boyce 1984, Nylin and Gotthard 1998,). However, what is less clear is how resource availability affects age-related within lifetime patterns of reproduction.

To determine the generality of terminal investment among species and across these environmental gradients, we test for terminal investment across three species of poecillids that experience a range of mortality and resource availability. We take advantage of populations of three different species that are naturally distributed across environmental gradients of mortality and resource availability. We address two questions across all three species. 1) Is reproductive allocation hyper-allometric relative to body size as individuals age (consistent with the terminal

investment hypothesis)? 2) Do mortality rates (i.e., predation environment) or resource availability influence the pattern of reproductive allocation with age? In other words, does high mortality or high resource availability enhance or diminish the expected terminal investment response?

Methods

Fishes in the family Poeciliidae have been used extensively for analysis of life history evolution (Evans et al. 2011). They are found in a wide variety of environments, and there is widespread variation in life history traits within and among species (Endler 1986). They are considered model organisms for the study of life history evolution, in part, because life histories vary in response to this broad range of environments (Evans et al. 2011).

Reproduction in poeciliids requires internal fertilization and females give birth to live young. Female poeciliids show indeterminate growth, so size is a good surrogate for age within populations allowing comparison of reproductive patterns of young and old individuals. We obtained age-specific (size-specific) life history data for three species of poeciliids, *Brachyrhaphis episcopi, Brachyrhaphis rhabdophora,* and *Poecilia reticulata* (Trinidadian guppies). Each of these species are found in high and low mortality environments and experience variation in resource availability as a consequence of annual wet and dry seasons (Rosen and Bailey 1963, Endler 1978, Reznick 1982, Jennions 2002, Johnson 2002, Langerhans 2007). The wet season provides valuable adult resources during flooding which we interpreted as increased resource availability compared to dry seasons (Winemiller 1993).

To investigate reproductive allocation, we used data from samples of *B. rhabdophora* collected from Costa Rica (see Johnson 2001), samples of *B. episcopi* collected from Panama (See Jennions 2006), and samples of *P. reticulata* collected from the isle of Trinidad (See

Reznick 1983). To calculate reproductive allocation we used the following variables - number of embryos, dry mass of embryos, developmental stage of embryos, and dry mass and length of females. We converted the specific developmental classification values to a common scale (Haynes 1995) for each species. As embryos progress in development they lose mass making it necessary to have all embryos compared as if they were at the same developmental stage. In the Haynes classification, stage three is the first fully-yolked, fertilized stage of development and stage 11 is a mature embryo with the yolk sac "mostly or completely absorbed". As not all embryos from the similar environments were at the same stage, we used regression (on pooled samples within similar predation environments and resource periods) to predict the mass of each individual embryo from each population as if it had been at stage three of development according to Haynes classification (Haynes 1995). This permitted us to compare all clutches without the confounding effect of stage of development at the time of collection.

Data for *B. rhabdophora* and *B. episcopi* were available for both wet (July-August) and dry (March-April) seasons in both high mortality and low mortality locations. Data for *P. reticulata* were available from high and low mortality locations but only during one season. We used female body mass (dry mass of eviscerated body) and clutch dry mass (See Reznick 1993, Johnson 2001, Jennions 2006) to characterize reproductive allocation. We used female dry mass as a surrogate of age to provide an analysis of patterns of allocation with age. For *B. rhabdophora* there were 537 observations from 22 locations during the dry season, and 209 observations from seven locations for the wet season. For *B. episcopi* there were 416 observations from 12 locations for the dry seasons, and 453 observations from 12 locations for the wet season. For *P. reticulata* there were 282 observations from 12 locations. Some observations were not used in the analysis because they seemed unlikely to be accurate (i.e. a

fish had a standard length of 33 mm but a dry mass of .001 mg), and most likely associated with recording errors. Seven observations from *B. rhabdophora* in the dry season, four from the *B. rhabdophora* in the wet season, eight from the *B. episcopi* in the dry season, three from the *B. episcopi* in the wet season, and five from *P. reticulata* were not included in the analysis because they were clear outliers.

Statistical Analysis

The data sets were hierarchical in that two reproductive traits (log cdm and log fdm) were measured on each of a sample of individual fish from several locations that exhibited either high or low predation. Thus traits were measured on individuals but predation levels were observed for locations. To reflect this hierarchy and make sure that differences due to locations were not confounded with differences due to predation states, we modeled the data using a mixed linear multivariate model (MLMM).

To properly characterize the relationship between female dry mass and clutch dry mass we used major-axis coefficients. This approach known as errors-in-variables or reduced major axis regression accounts for the potential for error on both the x and y axis in regression and thus is more appropriate for estimating the relationship between the two variables. To avoid bias due to 'regression towards the mean' (Stigler 1997 Warton and Weber 2002 Wright, Westoby, and Reich 2002), parameters of individual-level and location-level covariance matrices for the response variables were used to calculate major-axis coefficients. These coefficients were regarded as estimates of allometric coefficients for reproductive investment (Klingenberg 1996 p. 30-32), and evaluated as evidence consistent with or not consistent with terminal investment patterns. A slope of one between female dry mass and clutch dry mass would indicate an isometric relationship and no evidence for terminal investment. Terminal investment would be

indicated by a slope greater than one of the allometric coefficient suggesting that females allocate proportionately more to reproduction as they age (i.e., as body size increases). Using SAS Proc Mixed, we estimated and compared the allometric coefficients for each species by season by mortality environment combination. Because we did not have both wet and dry season samples for all three species, and because we were not interested in specific comparisons of parameter estimates among species, we analyzed species by season combinations of data (i.e., *B. rhabdophora* in the wet season). For each set of data we fit the following model. Both clutch dry mass and female dry mass were used as response variables. Mortality environment was used as a fixed effect and collection location and individual were used as random effects to account for among location variation and repeated measures (i.e., clutch dry mass and female dry mass) on individuals. To calculate allometric coefficients, model fitting was followed by post-processing of the estimated covariance matrices using the IML language of SAS (SAS Institute 2013). Allometric coefficients were calculated as coefficients of the eigenvectors of the individual-level covariance matrices. We used likelihood ratio tests to compare allometric coefficients between mortality environments (i.e, high predation versus low predation environments; Klingenberg 1996). To calculate confidence intervals we used the Delta method (Pawitan 2001).

Results

Allometric coefficients for all species were significantly greater than isometry (slope = 1) with slopes ranging from 1.27-1.89 (Table 1). As females age (and increase in size) they allocate proportionally more to reproduction compared to somatic mass. Old females allocated 2 – 5 fold more to reproduction compared to the isometric expectation (Fig. 1-5). Effects of mortality environment were not consistent across species. In *B. rhabdophora* high mortality environments

had significantly lower allometric coefficients than low mortality environments (Fig. 1, 2). In *B. episcopi* allometric coefficients did not differ between high and low mortality environments (Fig. 3, 4). In *P. reticulata* the pattern was opposite that in *B. rhabdophora;* high mortality environments had a significantly higher allometric coefficient than low mortality environments (Fig. 5). Effects of resource availability were consistent between the two species for which we have collections in both wet and dry seasons. In both *B. rhabdophora* and *B. episcopi* in high mortality environments allometric coefficients were lower during the season of high resource availability (i.e., wet season) compared to seasons of low resource availability. However, for both species in low mortality environments, there were no differences in allometric coefficients between high resource availability periods and low resource availability periods (Fig. 1-4).

Discussion

Female poeciliids grow throughout their lifetime, and thus increase in length and volume as they age. The concomitant change in reproductive allotment with age and growth determines whether lifetime allocation patterns are allometric or isometric. Notably, in this study all three species exhibited patterns consistent with terminal investment under all environmental conditions. Generality in pattern among these three species contrasts with the patterns exhibited by the closely related *Brachyrhaphis parismina* (Belk et al. 2011). In *B. parismina*, all populations exhibited an isometric pattern of reproductive allocation over the lifetime. In the literature there are several examples of organisms that exhibit terminal investment and those that do not. Some of those organism where terminal investment has been documented include Poeciliids (Billman and Belk, 2014), red deer (Clutton-Brock 1984), burying beetles (Creighton et al. 2009), red squirrels (Descamps et al. 2007), blue footed boobies (Velando, Drummond, and Torres 2006), Florida srub-jay (Wilcoxen, Boughton, and Schoech 2010), and rhesus macaques

(Hoffman et al. 2010) There has been other research demonstrating an absence of terminal investment in organisms such as pipefish (Billing, Rosenqvist, and Berglund 2007), bighorn sheep (Festa-Bianchet and King 2007), damselflys (Gonzalez-Tokman et al. 2013), mountain gorillas (Robbins et al. 2006), and chimpanzees and humans (Fessler et al. 2005).

Terminal investment may be precluded in high mortality environments or in environments with low resource availability. This suggests individuals in high mortality environments may not have expectations for future reproductive bouts and will invest more toward current reproduction. In high predation environments, individuals may always be experiencing a terminal life stage, meaning if predation is high we might see relatively more constant allocation across the individual's lifetime because the expectation for future reproductive bouts is lower in high mortality environments. Similarly, resource availability may affect the trade-off between current and future reproduction by ameliorating the cost to current reproduction. Empirical evidence demonstrates environments can affect the cost of reproduction trade-off (Mcnamara and Houston 1994, Trexler 1997). However, in these three species neither variation in mortality rates nor resource availability precluded patterns of terminal investment.

Additionally, environments with predators may exclude the ability to terminally invest due to the trade-off between the ability to escape predation and the optimal body shape for the livebearing mode of reproduction (Hassell et al. 2012). In livebearing females, the distention of the abdominal cavity can often change drastically during pregnancy, reducing escape speed and enhancing their susceptibility to predation (Wesner et al. 2011). This trade-off between abdominal size and escape speed demonstrates a possibility where terminal investment may not be possible due to environmental conditions. Furthermore, abiotic factors of environmental conditions like flow rates may induce a similar trade-off explaining the lack of terminal

investment in *B. parismina* (Belk et al. 2011)

There may be alternative explanations for the patterns we observed. For example, there may be some individuals that are simply better at resource acquisition than others and thus would be able to allocate more energy toward reproduction later in life. While the terminal investment hypothesis predicts increased allocation to current reproduction as expectations for future reproductive bouts decreases, it is also possible that the increase in energy allocation from older females is due to larger females having a competitive advantage to acquiring resources (Reznick et al. 200). If these females are able to acquire more resources then they may be allocating more toward reproduction due to this increase and may confound our results. However, laboratory studies of *G. affinis* females that were given more food resources proportionally increased allocation to reproduction compared to younger females (Vondracek et al. 1988). This proportional increase in consistent with the terminal investment hypothesis and our results.

An additional possible confounding result could surface if older females are more adept at avoiding predation than younger females. This would allow the older females to allocate more toward reproduction than younger females that would experience increased risk of predation correlated with increased cross sectional body surface area. This is an argument suggesting females allocate in response to space available and not due to a decrease in expectation for future reproductive bouts. However, the space in the body cavity is a function of how the muscles and organs are arraigned in conjunction with the body shape and unless there is a difference in rearrangement between young and old fish, the body cavity space should increase isometrically with female body mass and demonstrate a slope of 1 in the regression of female dry mass and clutch dry mass. Our results show slopes that are higher than 1 and suggest the reproductive allocation in young females is still below constraints imposed by body cavity space.

Additionally, the females in this study come from locations with many different predators and some locations experienced higher predation as larger (older) individuals. Some predators focused on adults, others juveniles and others preyed on all sizes. Additionally, the number of observations and the different localities sampled will ameliorate the effects of any small aggregate of individuals.

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Table

Table 1 Summary of tests for isometry of allometric coefficients across three species of poeciliids in high and low mortality environments (i.e., predator) and high and low resource availability (i.e., wet versus dry season). The allometric coefficient is the slope of the relationship between clutch dry mass and female dry mass. The last two columns report the outcome of tests for isometry (i.e., Different than 1) and the test for differences between high and low mortality environments (i.e., Different than each other).

Species	Resource availability	Predator	Allometric coefficient	SE	95% CI	Different than 1	Different than each other
B.rhabdophora	Low	No	1.89	0.09	1.80-1.98	Yes	Yes
	Low	Yes	1.56	0.08	1.47-1.68	Yes	
	High	No	1.86	0.14	1.58-2.15	Yes	Yes
	High	Yes	1.27	0.04	1.17-1.36	Yes	
B. episcopi	Low	No	1.41	0.06	1.29-1.53	Yes	No
	Low	Yes	1.32	0.05	1.20-1.44	Yes	
	High	No	1.52	0.06	1.39-1.66	Yes	No
	High	Yes	1.48	0.06	1.36-1.60	Yes	
P. reticulata	Low	No	1.43	0.09	1.25-1.62	Yes	Yes
	Low	Yes	1.71	0.11	1.50-1.93	Yes	

Figure Legend

Figure 1. Female dry mass (log 10) by clutch dry mass (log 10) by predation of *B. rhabdophora* during the dry season comparing high and low mortality environments. Dark line is low mortality, dotted line is high mortality, and light line is isometry. Units are logged mg.

Figure 2. Female dry mass (log 10) by clutch dry mass (log 10) by predation of *B. rhabdophora* during the wet season comparing high and low mortality environments. Dark line is low mortality, dotted line is high mortality, and light line is isometry. Units are logged mg.

Figure 3. Female dry mass (log 10) by clutch dry mass (log 10) by predation of *B. episcopi* during the dry season comparing high and low mortality environments. Dark line is low mortality, dotted line is high mortality, and light line is isometry. Units are logged mg.

Figure 4. Female dry mass (log 10) by clutch dry mass (log 10) by predation of *B. episcopi* during the wet season comparing high and low mortality environments. Dark line is low mortality, dotted line is high mortality, and light line is isometry. Units are logged mg.

Figure 5. Female dry mass (log 10) by clutch dry mass (log 10) by predation of *P. reticulata* comparing high and low mortality environments. Dark line is low mortality, dotted line is high mortality, and light line is isometry. Units are logged mg.

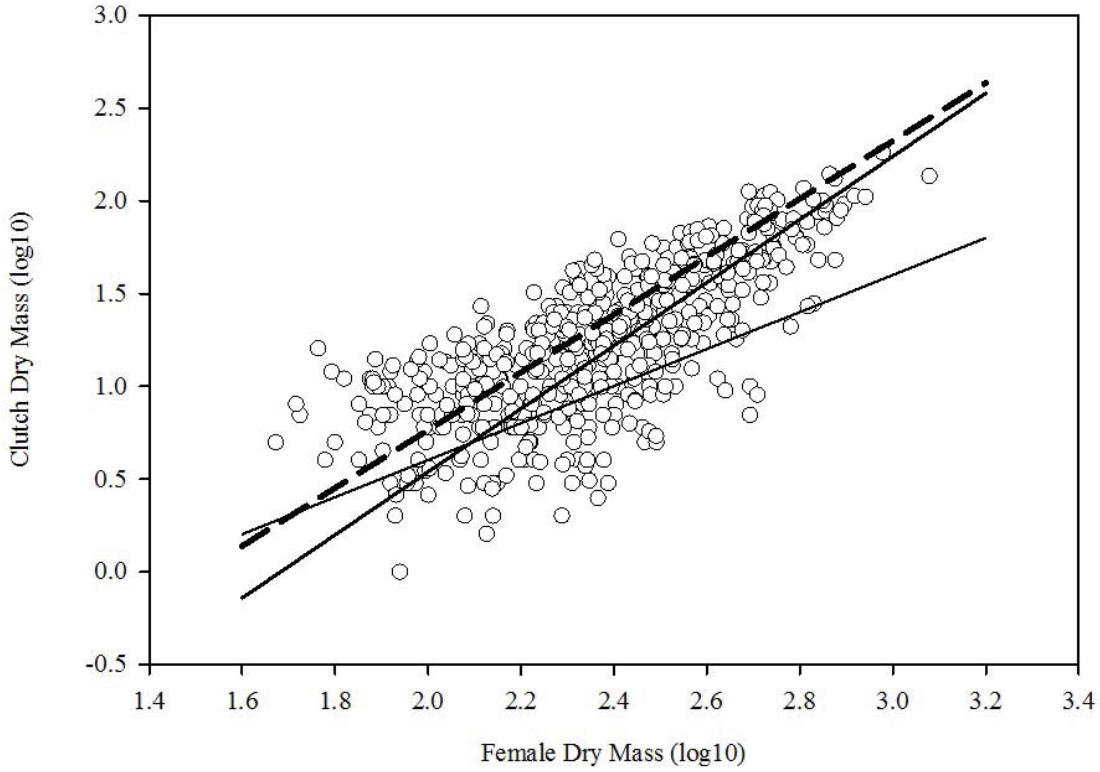
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
Clutch Dry Mass (log10)
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2
3.4
Female Dry Mass (log10)

Figure 1

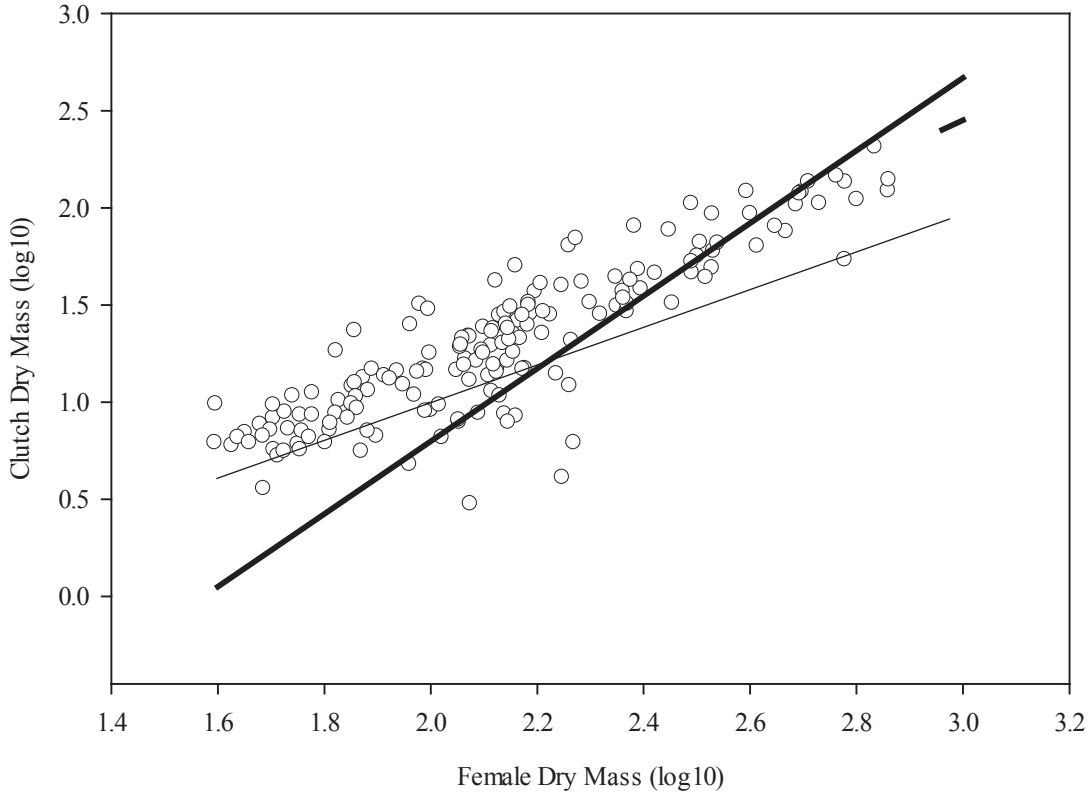
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Clutch Dry Mass (log10)
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2
Female Dry Mass (log10)

Figure 2

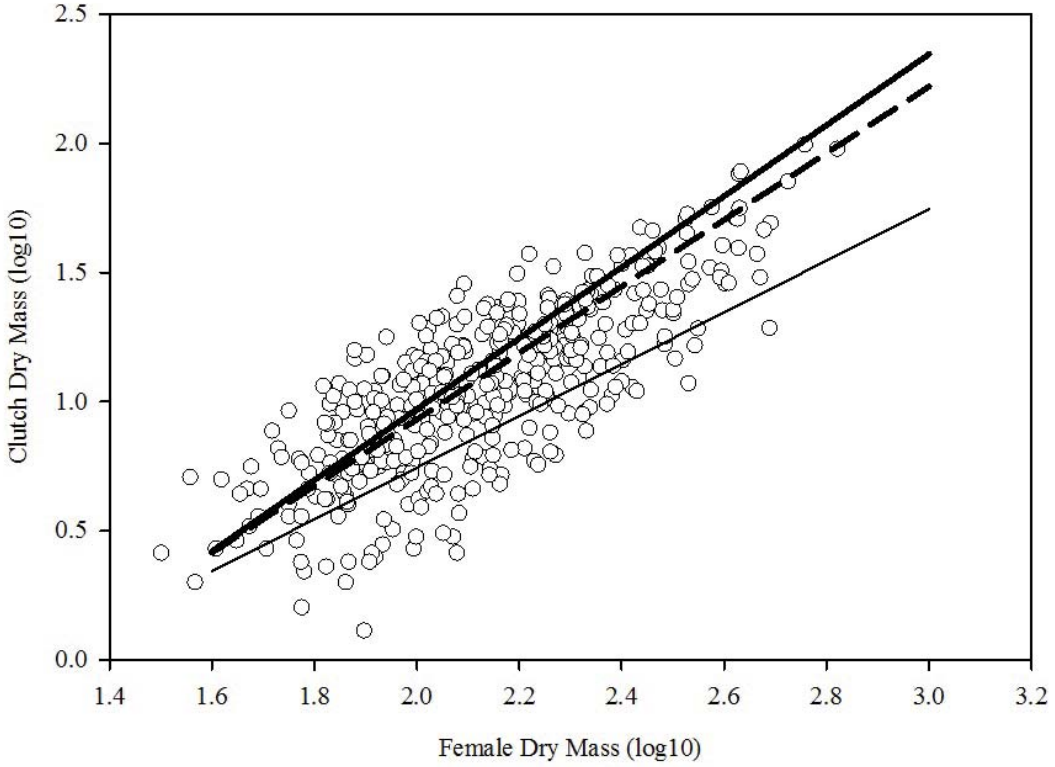
Clutch Dry Mass (log10)
Female Dry Mass (log10)
2.5
2.0
1.5
1.0
0.5
0.0
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2

Figure 3

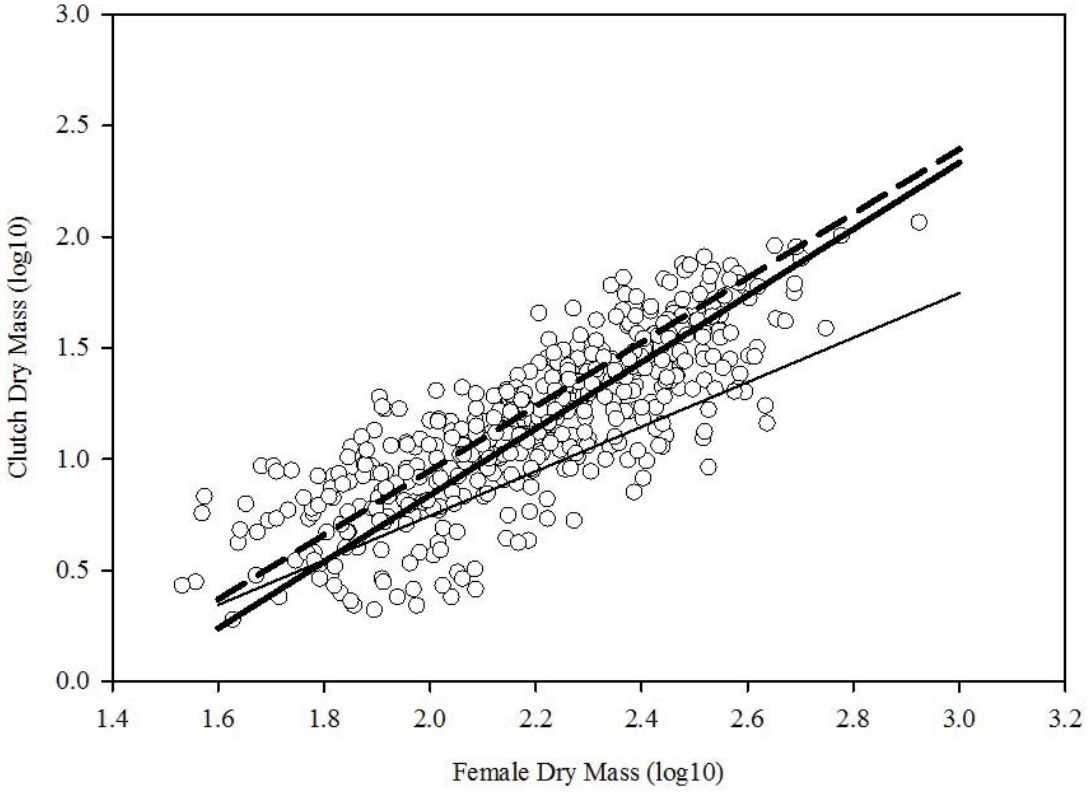
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Clutch Dry Mass (log10)
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2
Female Dry Mass (log10)

Figure 4

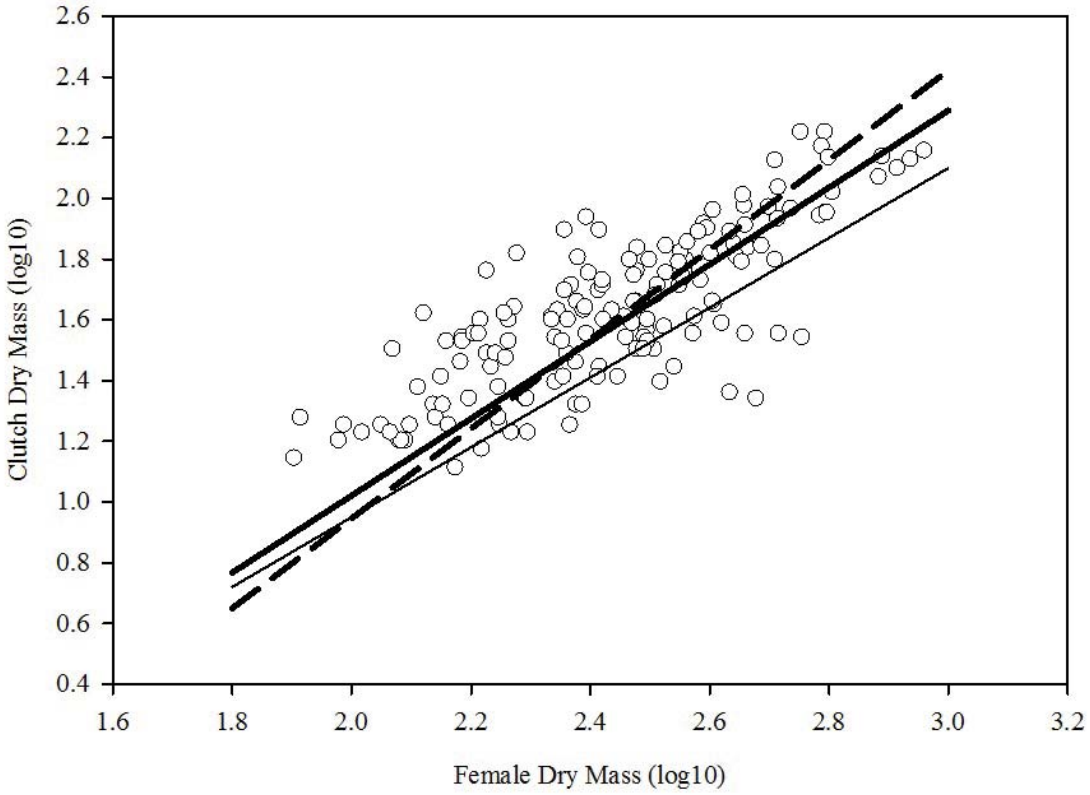
Clutch Dry Mass (log10)
Female Dry Mass (log10)
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2

Figure 5