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Length–mass relationships for adult aquatic and terrestrial invertebrates in a California watershed

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Abstract. We collected 541 invertebrate specimens in riparian and upland habitats of the South Fork (SF) Eel River, California, USA, representing 12 orders and 55 families, and including adults of both aquatic and terrestrial origin. We fitted a power function to this data set at 4 taxonomic levels: 1) the entire pooled sample, 2) composite samples of aquatic and terrestrial taxa, 3) individual orders, and 4) individual families for which there were adequate data ($n > 8$; 24 families). Coefficients of determination (R^2) for length–mass relationships generally increased with increasing taxonomic specificity. Composite samples of aquatic and terrestrial taxa had significantly different length–mass relationships, with dry mass increasing faster with length in terrestrial taxa. Differences in length–dry mass relationships between aquatic and terrestrial taxa appeared to result from significantly higher slopes for terrestrial taxa in length–width relationships, and significantly lower slopes in length–water content relationships. Our results suggest that the use of terrestrial regressions to estimate aquatic insect biomass flux in riparian habitats overestimates both the absolute magnitude of biomass flux as well as its relative importance to insect standing stocks. Development of unique regression algorithms for adult aquatic insect taxa increases the accuracy of aquatic insect biomass estimates in terrestrial habitats.

Key words: length–mass regression, body size, biomass estimation, river–watershed exchange, energy flux.

Biomass is a key variable in quantifying a variety of energetic processes in food webs, ranging from individual consumption and bioenergetics (e.g., Kitchell et al. 1974) to the spatial transfer of energy between habitats (e.g., Polis and Hurd 1995). Insects often play key roles in these processes because of their high abundance and biomass in both aquatic and terrestrial food webs (Gullan and Cranston 1994). Unfortunately, large samples and semidestructive sampling often make direct measurements of invertebrate biomass difficult or impossible. Invertebrate biomass can be estimated from known relationships with more easily measured body size parameters. The most widely accepted technique for biomass estimation involves regression of dry mass on body length (Benke et al. 1999). However, despite numerous compilations of length–mass relationships for both terrestrial invertebrates (e.g., Rogers et al. 1976, 1977, Schoener 1980, Sample et al. 1993, Hawkins et al. 1997, Lang et al. 1997) and larvae of freshwater insects (Smock 1980, Burgherr and Meyer 1997, Benke et al. 1999, Johnston and Cunjak 1999), there are few published relationships for adult aquatic insects. To our knowledge, regression equations for adults have only been published for 3 aquatic orders—Diptera (Sample et al. 1993, Rogers et al. 1977) and Plecoptera and Trichoptera (Sample et al. 1993).

Because adult aquatic insects may be important energy conduits between streams and adjacent riparian habitats (Jackson and Fisher 1986, Gray 1989, Sabo 2000, Nakano and Murakami 2001, Sabo and Power 2002), the paucity of published length–mass relationships for many insect groups may prohibit studies of energy flow between these 2 habitats. Currently, determination of adult aquatic insect biomass in a number of unstudied taxa depends on direct measurement (Jackson and Fisher 1986), or estimation of length–dry mass relationships derived from similar terrestrial insects or larvae of aquatic insects. Adult and larval aquatic insects often differ considerably in their length–mass relationships as a result of morphological and water content differences (Rogers et al. 1976, Smock 1980); adult aquatic and terrestrial invertebrates also may differ for similar reasons (Smock 1980). If differences in length–mass relationships between adult aquatic and terrestrial taxa exist, specific regressions for adult aquatic insects are essential for estimating their biomass.

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The purpose of our study was to compare the length–mass relationships of adult aquatic and terrestrial invertebrates collected within a northern California watershed. To do so, we compared regression slopes of composite samples of aquatic invertebrates with those of terrestrial taxa. We further analyzed *length–width* and *length–water content* relationships for aquatic and terrestrial invertebrate taxa to evaluate how differences in shape and water content contributed to variability in length–mass relationships between aquatic and terrestrial taxa. Last, we applied 3 different regression models varying in taxonomic specificity to adult insects captured along the stream margin to evaluate the consistency of models in estimating the magnitude of aquatic biomass transfer to surrounding riparian habitats.

Methods

Study area

Our study took place along a 4-km reach of the South Fork (SF) of the Eel River, Mendocino County, California, USA (lat 39°44′N, long 123°39′W). This river flows through old-growth Douglas fir (*Pseudotsuga menziesii*) and coastal redwood (*Sequoia sempervirens*) forest within the outer coast range of northern California. We sampled invertebrates within 100 m of the river in 3 distinct habitats within the SF Eel watershed: 1) riparian and upland forest, 2) open riparian cobble bars, and 3) grassy meadows on upland river terraces. Detailed accounts of these habitats are given by Kotanen (1997), Levine (1999), and Sabo (2000).

Sample collection

Invertebrate samples were collected from June to August in 1998 and 1999. Arthropods were caught by hand, in dry pitfall traps, or by sweeping an insect net through vegetation. Specimens were transferred to sample vials and then refrigerated until processing (within 72 h). We measured invertebrate body lengths under a dissecting microscope to the nearest 0.1 mm; appendages such as antennae or cerci were excluded from measurements. We also measured the width of the thorax or abdomen, whichever was wider. We also weighed fresh specimens to the nearest 0.01 mg to obtain wet mass. Specimens were dried at 65°C for 24 to 48 h and then were reweighed to determine dry masses to the nearest 0.01 mg.

Analyses were based on 541 specimens in 55 families and 12 orders (Table 1). Of these 12 orders, 5 were aquatic (Ephemeroptera, Lepidoptera (*Petrophila* spp.), Odonata, Plecoptera, and Trichoptera), 6 were terrestrial (Araneae, Coleoptera, Homoptera, Hymenoptera, Orthoptera, and Microcoryphia), and 1 order (Diptera) had both terrestrial and aquatic representatives. Specimens were classified as either riverine (aquatic) or riparian (terrestrial); identification to order was generally adequate for this classification. Finer taxonomic resolution was needed to resolve larval habitat origin for dipterans, which had taxa with terrestrial (e.g., Asilidae), aquatic (e.g., most Chironomidae), and semiaquatic (e.g., Athericidae) larvae. We classified the dipteran families Athericidae, Chironomidae, Culicidae, Ephydridae, Tabanidae, and Tipulidae as riverine. These families include taxa with truly aquatic larvae or those from semiaquatic habitats (e.g., riverine side pools or damp soil, Borror et al. 1997). We classified the dipteran families Asilidae, Bombyliidae, Dolichopodidae, Heleomyzidae, Muscidae, and Syrphidae as terrestrial. The first 5 of these families have larvae that live in leaf litter, under bark, in insect nests, in damp soil not associated with river margins, or occur as internal parasites of other animals (Borror et al. 1997). Several representative syrphid genera have aquatic habitat preferences as larvae, but many taxa inhabit more polluted waters (Borror et al. 1997).

Data analysis

We fit data from the complete pooled data set ($n = 541$), the composite aquatic and terrestrial data sets ($n = 178$ and 363, respectively), and the 12 individual orders to the power function:

$$W = aL^b$$

where W is dry mass (mg), L is length (mm), and a and b are fitted parameters describing the allometric relationship between these variables. Parameters were fit using nonlinear least-squares regression, with starting values of 0.03 and 2.62, and bounds of 0.001 to 1.5 and 1.0 to 4.5 for a and b, respectively. Slopes of length–dry mass regressions for aquatic and terrestrial taxa were compared using the interaction term

TABLE 1. Sample size of individual orders and families included in the analysis.

Taxon	*n*
Aquatic	
Diptera	61
Brachycera	28
Athericidae	18
Ephydridae	5
Tabanidae	5
Nematocera	33
Chironomidae	8
Culicidae	17
Tipulidae	8
Ephemeroptera	45
Lepidoptera (Pyrallidae)	24
Odonata	45
Aeshnidae	6
Coenagrionidae	17
Cordulegastridae	6
Gomphidae	15
Macromiidae	1
Plecoptera	45
Chloroperlidae	12
Perlidae	11
Pteronarcyidae	22
Trichoptera	19
Limnephilidae	10
Hydropsychidae	9
Terrestrial	
Araneae	23
Lycosidae	22
Salticidae	1
Coleoptera	119
Bostrichidae	17
Buprestidae	4
Byrrhidae	1
Cantharidae	1
Carabidae	29
Cerambycidae	2
Chrysomelidae	5
Ciccindelidae	6
Coccinellidae	12
Curculionidae	4
Dermestidae	1
Meloidae	6
Melyridae	8
Mordelidae	7
Nitidulidae	1
Scarabaeidae	5
Staphylinidae	10
Homoptera	23
Cicadidae	10
Cicadellidae	13
Hymenoptera	54
Anthophoridae	4
Apidae	10
Chrysididae	1
Formicidae	9
Ichneumonidae	2
Sphecidae	9
Vespidae	19
Orthoptera	42
Acrididae	11
Gryllacrididae	7
Tetrigidae	24
Microcoryphia	11
Diptera	30
Brachycera	30
Asilidae	9
Bombyliidae	10
Calliphoridae	1
Dolichopodidae	1
Heleomyzidae	1
Muscidae	5
Syrphidae	3

in an analysis of covariance (ANCOVA) on ln-transformed lengths and masses (Winer et al. 1991, Goldberg and Scheiner 1993). We also compared the slopes of length vs water content (wet mass–dry mass)/(wet mass) and length vs width regressions of aquatic and terrestrial taxa. In this analysis, we used ln-transformed lengths and arcsine-square root-transformed proportional water content to correct for non-normality (Zar 1998). Significant interactions between habitat origin and body length on width, or origin and length on water content would suggest that body shape or water content varied differently with body length between aquatic and terrestrial taxa.

Influence of taxonomic level on predicted biomass

We used data from sticky traps to test the influence of taxonomic level on the predicted biomass of aquatic and terrestrial invertebrates caught at the land–water interface. We set a total of 73 sticky traps within 10 m of the river on 7 discrete cobble bar habitats for a period of 5 d (15–20 May 1997). Traps consisted of a 612 cm^2 acetate sheet covered with a thin coating of Tanglefoot®. We hung traps at a height of 1.5 m on rebar posts. Upon collection, traps were covered with cellophane and transported to the laboratory, where they were stored at 12°C. All captured inverte-

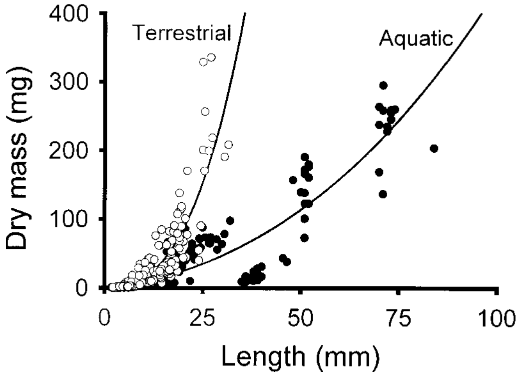

FIG. 1. Length (mm) vs dry mass (mg) for adult invertebrates of aquatic (closed circles) and terrestrial (open circles) origin, within the South Fork Eel River watershed. Models and parameter estimates are: $y = 0.032x^{2.63}$ and $R^2 = 0.81$ for terrestrial taxa and $y = 0.11x^{1.79}$ and $R^2 = 0.87$ for aquatic taxa. Slopes for the linear regressions on ln-transformed data differed significantly (terrestrial > aquatic) in ANCOVA ($F = 52.84$, df = 1,537, $p < 0.001$).

brates were identified and their lengths measured to the nearest 0.1 mm. Three different regression models were applied to this data set: 1) *terrestrial,* in which the composite terrestrial model was applied to all specimens, 2) *origin-specific,* in which models derived from composite aquatic and terrestrial data sets were applied to taxa from the corresponding habitat, and 3) *order-specific,* in which collective biomass was determined by applying unique regression models for each order of specimens in our sample. We used our terrestrial regression rather than published models because it was nearly identical to other commonly cited composite models for terrestrial taxa (e.g., Rogers et al. 1976: a = 0.0305, b = 2.62). For the order-specific model, we applied origin-specific models to all taxa lacking order-level regressions (i.e., for Hemiptera, Megaloptera, terrestrial Lepidoptera).

Results

Aquatic–terrestrial comparisons

Adult invertebrates of terrestrial and aquatic origin had divergent length–mass relationships when analyzed as composite samples from each habitat (Fig. 1). Although the pooled terrestrial–aquatic data set produced a relatively high coefficient of determination (R^2= 0.71), R^2 values were higher for regressions when aquatic and terrestrial samples were considered separately (0.87 and 0.81, respectively), and highest for regressions on order-level data sets (Table 2). Dry mass increased significantly faster with length for terrestrial (vs aquatic) taxa ($F = 52.84$, df = 1,537, $p < 0.001$), with differences in relationships seemingly a function of differences in body shape (Fig. 2) and water content (Fig. 3). Terrestrial taxa increased in width significantly faster with length (and were less linear in shape) than aquatic taxa ($F = 6.32$, df = 1,301, $p < 0.05$). Further, water content of aquatic insects increased with length significantly faster than that of terrestrial invertebrates ($F = 29.5$, df = 1,471, $p < 0.005$). Only aquatic taxa had a non-zero slope for the regression of length on water content ($F = 86.2$, df = 1,209, $p < 0.005$, aquatic; $F = 0.3$, df = 1,262, $p > 0.50$, terrestrial; Fig. 3).

In contrast to differences between length–mass relationships of aquatic and terrestrial invertebrates in composite samples, values for parameters a and b were not consistently different between aquatic and terrestrial orders (Table 2). Average values of a and b ranged from 0.005 to 0.56 and 1.56 to 3.33, respectively, in order-level regressions, and were not significantly different between aquatic and terrestrial taxa (Kolmogorov–Smirnov test, $p > 0.8$ for a and b).

Two potential sources of bias in our analysis of composite samples were 1) unequal size distributions of aquatic and terrestrial invertebrates within the sample (e.g., only aquatic taxa had lengths >30 mm, see Fig. 1), and 2) unequal sample size within individual orders. To remove the potential bias of outlying aquatic taxa, we excluded all taxa >30 mm in length from the data set (exclusively Odonata and Plecoptera) and reanalyzed this adjusted data set using ANCOVA. Removal of these outlying groups did not alter the results: slopes of length–mass relationships were still significantly higher for terrestrial taxa ($F = 26.87$, df = 1,447, $p < 0.005$). To remove the potential bias of unequal sample size within orders (e.g., $n = 23$ and 119 for Homoptera and Coleoptera, respectively), we reanalyzed each composite data set using average length and mass within individual orders ($n = 6$ and 7 for aquatic and terrestrial taxa, respectively) and then compared adjusted slopes. Averaging did not significantly alter slopes of length–mass relationships for either aquatic ($F = 0.01$, df = 1,241, $p > 0.9$) or terrestrial ($F = 0.7$, df = 1,305, $p > 0.4$) data sets.

TABLE 2. Parameters and R^2 values for 3 regression models. We regressed length (mm) on dry mass (mg) for the 12 individual orders collected in our sample, for composite samples of aquatic (= Aquatic composite) and terrestrial (= Terrestrial composite) arthropods, and all specimens combined (= Pooled).

Taxon	a (SE)	b (SE)	R^2
Aquatic			
Ephemeroptera	0.014 (0.001)	2.49 (0.3)	0.89
Lepidoptera[a]	0.012 (0.02)	2.69 (0.87)	0.82
Odonata	0.14 (0.02)	2.27 (0.25)	0.90
Plecoptera	0.26 (0.15)	1.69 (0.18)	0.95
Trichoptera	0.01 (0.01)	2.9 (0.39)	0.92
Average[b]	0.09 (0.05)	2.41 (0.21)	0.90
Terrestrial			
Coleoptera	0.04 (0.14)	2.64 (0.06)	0.95
Homoptera	0.005 (0.001)	3.33 (0.5)	0.93
Hymenoptera	0.56 (0.64)	1.56 (0.4)	0.75
Orthoptera	0.03 (0.02)	2.55 (0.15)	0.95
Araneae	0.05 (0.01)	2.74 (0.11)	0.98
Microcoryphia	0.05 (0.03)	2.06 (0.34)	0.97
Average[b]	0.12 (0.09)	2.48 (0.25)	0.92
Other[c]			
Diptera	0.04 (0.04)	2.26 (0.33)	0.67
Brachycera	0.006 (0.007)	3.05 (0.36)	0.85
Nematocera	0.1 (0.06)	1.57 (0.2)	0.90
Grand average (by Order)[b]			
Aquatic composite	0.1 (0.04)	2.37 (0.15)	0.91
Terrestrial composite	0.11 (0.04)	1.79 (0.08)	0.87
Pooled	0.03 (0.01)	2.63 (0.10)	0.81
	1.1 (0.2)	1.24 (0.05)	0.71

[a] *Petrophila* spp.

[b] SEs derived from differences among taxa for the same parameter. All other SEs estimated directly from least-squares regression

[c] Taxa with aquatic, semiaquatic, and terrestrial larvae

Biomass flux estimates

Estimates of the magnitude of aquatic insect biomass flux from the river to adjacent riparian habitats made with the 3 regression models (terrestrial, origin-specific, and order-specific) differed significantly ($F = 4.59$, df = 2,216, $p < 0.01$, Fig. 4). The terrestrial model generated higher estimates than origin- and order-specific models (Tukey's test, $p < 0.05$ for both contrasts), although estimates did not differ between these 2 models ($p > 0.9$). More importantly, there was disagreement among the models with respect to the relative importance of aquatic and terrestrial biomass sampled from SF Eel near-river habitats (Fig. 4). The relative importance of aquatic insect biomass differed significantly among models (2-way ANOVA, origin × model interaction: $F = 4.16$, df = 2,432, $p < 0.05$). Whereas order- and origin-specific models predicted higher relative terrestrial biomass, the terrestrial regression model predicted higher relative aquatic biomass when applied to aquatic and terrestrial specimens in the data set.

Discussion

Length–mass regression is the most commonly used technique for estimating biomass from samples when direct measurement is neither possible nor practical. However, because there are very few published regression equations for adult aquatic insects, estimates of adult aquatic insect biomass often are based on equations for composite samples of terrestrial invertebrates (Rogers et al. 1976) or models describing aquatic larvae, which have strongly contrasting body

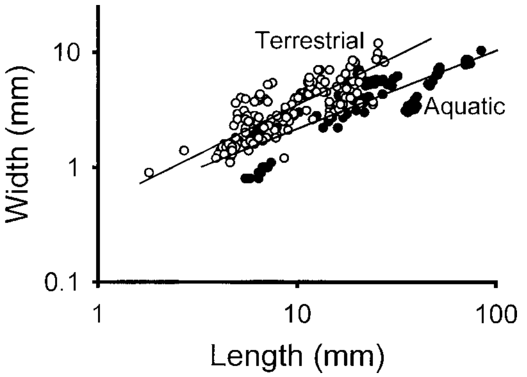

FIG. 2. Length–width relationships for adult invertebrates of aquatic (closed circles) and terrestrial (open circles) origin. Slopes of best-fit lines for terrestrial (upper line) and aquatic (lower line) taxa differed significantly (terrestrial > aquatic) in ANCOVA (F = 6.32, df = 1,301, $p < 0.05$). Regression models are: ln (y) = −0.7 + 0.84 [ln (x)], $R^2 = 0.68$ for terrestrial taxa and ln (y) = −0.88 + 0.69 [ln (x)], $R^2 = 0.77$ for aquatic taxa.

shapes (Smock 1980, Benke et al. 1999). Previous studies suggest that larval length–mass relationships differ significantly from those of adults of the same species (Rogers et al. 1977, Smock 1980). Moreover, discrepancies between the length–mass relationships of aquatic and terrestrial insects may also arise from inherent differences in water content and the degree of chitinization between these 2 groups of insects (Smock 1980).

To our knowledge, data in this paper represent the 1st published length–mass relationships for adults of 3 aquatic orders, Ephemeroptera, aquatic Lepidoptera of the genus Petrophila, and Odonata. We also provide regression equations for 24 families within these and the other orders examined in this study (Table 3). Our results suggest that adult aquatic and terrestrial invertebrates have significantly different length–dry mass relationships, with terrestrial invertebrates showing steeper length–dry mass and length–width relationships, but less-steep length–water content relationships than adult aquatic insects. Dry mass appears to increase faster with increasing body length in terrestrial taxa because these animals have higher relative body volume and less of this body volume consists of water. Consequently, we observed substantial differences between regression models in their prediction of absolute aquatic insect biomass, as well as in the relative fraction of invertebrate biomass made up by aquatic taxa in near-river habitats. Estimates of aquatic insect biomass were highest using a composite regression based only on terrestrial taxa (e.g., similar to applying the terrestrial regression of Rogers et al. 1976 to terrestrial and aquatic taxa). If finer-level taxonomic resolution in length–mass regressions yields more accurate biomass predictions (Smock 1980, Benke et al. 1999), our results suggest that general terrestrial regressions may grossly overestimate adult aquatic insect biomass. Terrestrial regressions further overestimate the relative importance of aquatic insect fluxes in riparian settings. In contrast, origin- and order-specific models did not differ signif-

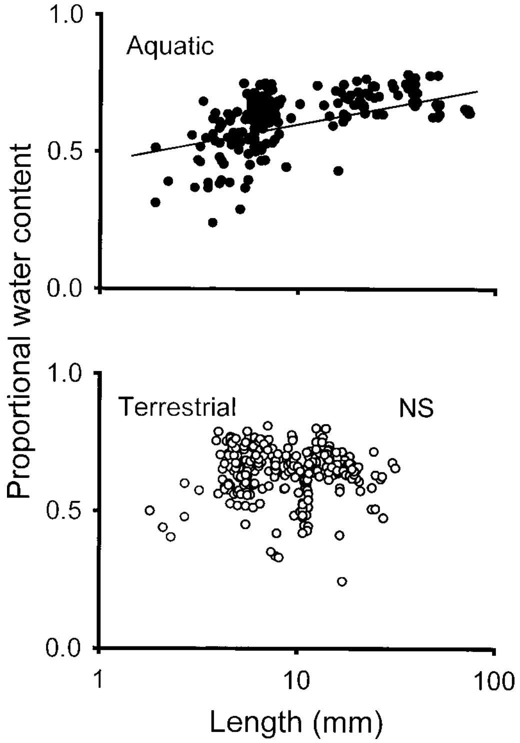

FIG. 3. Invertebrate length vs water content (e.g., [wet mass–dry mass)/wet mass]). Slopes differed significantly between these 2 groups of taxa (aquatic > terrestrial) in ANCOVA (F = 29.5, df = 1,471, $p < 0.005$). Regression slopes differed significantly from 0 in aquatic (F = 86.2, df = 1,209, $p < 0.005$) but not terrestrial taxa (F = 0.3, df = 1,262, $p > 0.5$). Models for individual regressions are: ln y = 0.77 + 0.063 [ln (x)] for aquatic taxa, and ln (y) = 0.94 − 0.006 [ln (x)] for terrestrial taxa. NS = not significant.

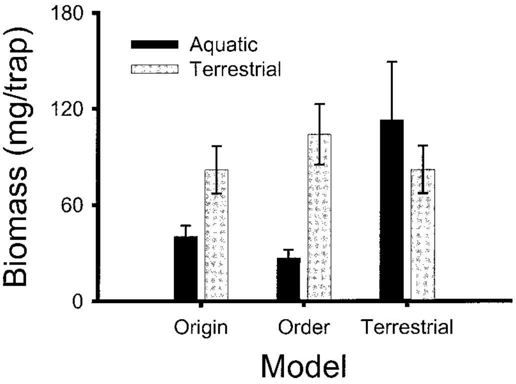

FIG. 4. Estimation of relative biomass (mean ± 1 SE) of aquatic and terrestrial invertebrates caught on sticky traps from the South Fork Eel River, May 1997. Biomass was estimated by applying origin-specific aquatic and terrestrial (= Origin), order-specific (= Order), or terrestrial regression equations (= Terrestrial) to the same data set. Terrestrial biomass estimates in terrestrial and origin-specific models are from the same algorithm (i.e., origin-specific regression for terrestrial specimens).

icantly in predicting absolute aquatic insect biomass, and both models predicted similar patterns of relative aquatic and terrestrial invertebrate biomass. Further investigation is needed on length–mass relationships within aquatic families and orders not studied here. Nevertheless, comparison of the performance of regression models at predicting aquatic insect biomass suggests that an origin-specific regression equation for aquatic insects may provide a more accurate tool for predicting the biomass of adult aquatic insects than previously published algorithms derived from terrestrial taxa.

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TABLE 3. Parameters and R^2 values for regressions of mass on length for individual families (excluding cases where $n \leq 8$).

Family	n	a (SE)	b (SE)	R^2
Acrididae	11	0.085 (0.107)	2.274 (0.379)	0.97
Apidae	10	0.006 (0.041)	3.407 (2.471)	0.81
Asilidae	9	0.38 (2.625)	1.5 (2.469)	0.74
Athericidae	18	0.164 (0.132)	1.558 (0.427)	0.98
Bombyliidae	10	0.007 (0.011)	3.337 (0.676)	0.95
Bostrichidae	17	0.039 (0.017)	2.764 (0.252)	0.99
Carabidae	29	0.072 (0.011)	2.401 (0.051)	0.99
Chloroperlidae	12	0.005 (0.006)	2.732 (0.622)	0.98
Cicadidae	10	0.004 (0.012)	3.373 (0.85)	0.93
Cicadellidae	13	0.079 (0.25)	2.229 (1.538)	0.99
Coccinellidae	12	0.343 (0.618)	1.5 (0.955)	0.91
Coenagrionidae	17	0.001 (0.009)	2.672 (2.535)	0.90
Cucilidae	17	0.032 (0.018)	2.038 (0.391)	0.95
Formicidae	9	0.027 (0.027)	2.666 (0.595)	0.93
Gomphidae	15	0.001 (0.009)	3.012 (2.328)	0.92
Hydropsychidae	9	0.049 (0.105)	2.295 (1.078)	0.96
Microcoryphia[a]	11	0.048 (0.032)	2.056 (0.34)	0.97
Perlidae	11	0.008 (0.014)	2.819 (0.593)	0.98
Pyralidae	24	0.012 (0.021)	2.695 (0.868)	0.82
Pteronarcyidae	22	0.506 (0.507)	1.5 (0.306)	0.97
Sphecidae	9	0.166 (0.184)	1.797 (0.365)	0.97
Staphylinidae	10	0.001 (0.001)	4.026 (0.288)	0.99
Tetrigidae	24	0.358 (0.395)	1.5 (0.432)	0.90
Vespidae	19	0.001 (0.002)	3.723 (0.798)	0.95

[a] Order

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