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Comparing Life Histories across Taxonomic Groups in Multiple Dimensions: How Mammal-Like Are Insects?

Adam T. Bakewell,^{1,*} Katie E. Davis,¹ Robert P. Freckleton,² Nick J. B. Isaac,³
and Peter J. Mayhew¹

1. Department of Biology, University of York, Heslington, York YO10 5DD, United Kingdom; 2. Department of Animal and Plant Sciences, University of Sheffield, Alfred Denny Building, Western Bank, Sheffield S10 2TN, United Kingdom; 3. Centre for Ecology and Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire OX10 8BB, United Kingdom

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ABSTRACT: Explaining variation in life histories remains a major challenge because they are multidimensional and there are many competing explanatory theories and paradigms. An influential concept in life-history theory is the fast-slow continuum, exemplified by mammals. Determining the utility of such concepts across taxonomic groups requires comparison of the groups' life histories in multidimensional space. Insects display enormous species richness and phenotypic diversity, but testing hypotheses like the fast-slow continuum has been inhibited by incomplete trait data. We use phylogenetic imputation to generate complete data sets of seven life-history traits in orthopterans (grasshoppers and crickets) and examine the robustness of these imputations for our findings. Three phylogenetic principal components explain 83%–96% of variation in these data. We find consistent evidence of an axis mostly following expectations of a fast-slow continuum, except that “slow” species produce larger, not smaller, clutches of eggs. We show that the principal axes of variation in orthopterans and reptiles are mutually explanatory, as are those of mammals and birds. Essentially, trait covariation in Orthoptera, with “slow” species producing larger clutches, is more reptilelike than mammal-like or birdlike. We conclude that the fast-slow continuum is less pronounced in Orthoptera than it is in birds and mammals, reducing the universal relevance of this pattern and the theories that predict it.

Keywords: Orthoptera, fast-slow continuum, life history, phylogenetic comparative methods.

Introduction

The life history of an organism describes the way it develops and reproduces, as well as its expected life span. Life histories represent much phenotypic diversity and are strongly related

to ecology and organismal fitness, so the explanation of life-history variation has been one of the major challenges in ecology and evolutionary biology (Stearns 1992; Charnov 1993; Roff 2002). A central tenet of life-history theory is the operation of trade-offs between the various life-history components; individuals must invest resources competitively into growth, maintenance, and reproduction (Stearns 1992; Braendle et al. 2011). One of the major aims of life-history research is to understand how, given different ecological challenges, trade-offs in investment have formed patterns of covariation between life-history traits (Stearns 1992). Some 45 possible trade-offs among life-history traits were listed in Stearns's (1992) influential book, and many more potentially exist. These include balances between investment in traits (e.g., current reproduction vs. survival, or parental growth), and investment within the same traits over time (e.g., current vs. future reproduction).

Over evolutionary time, selection should optimize investment into different life-history traits to increase fitness. Many classical questions about life-history variation focus on a single trait, such as clutch size (Lack 1947), life span (Medawar 1952), or frequency of reproductive events (Cole 1954). However, it has also long been recognized that organismal life histories can be quantified in multiple dimensions and that broad explanations of covarying suites of traits may also be possible. Attempted explanations include r/K selection theory, which posits that variation in life-history strategies is a consequence of density-dependent versus density-independent selection (MacArthur and Wilson 1967; Pianka 1970); CSR theory in plants, which explains variation as adaptations to environments with combinations of either high or low levels of stress and disturbance leading to three extreme strategies (competitors, stress tolerators, and ruderals; Grime 1977; Grime and Pierce 2012) and Charnov's theory for mammals (details below; Charnov 1991; Harvey and Purvis 1999). There is also a suite of demographic models that predict how the rate and timing of investment in reproduction responds to forces such as extrinsic mortality, resource availability, the form of

* Corresponding author; email: ab1348@york.ac.uk.

ORCID: Bakewell, <https://orcid.org/0000-0001-5289-2846>; Davis, <https://orcid.org/0000-0002-9235-7853>; Mayhew, <https://orcid.org/0000-0002-7346-6560>.

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population regulation, and stochasticity in vital rates (Stearns 1992; Reznick et al. 2002).

Parallel with these explanatory paradigms and theories has been the development of empirical generalizations of life-history covariation, which describe how life-history traits are expected to intercorrelate. Prominent among interspecific paradigms has been the fast-slow continuum, which suggests that species fall somewhere between the “fast,” with high fecundity, short generation times, early reproduction, short life spans, and small offspring and adult body sizes; and “slow” species with the opposite suite of traits (Stearns 1983; Braendle et al. 2011). The term “fast-slow continuum” is thought to have first been coined by Sæther (1987). It largely replaced the term “ r/K selected” after r/K selection theory fell out of favor as an explanation of trait covariation but where researchers still needed to refer to trait patterns predicted by that theory (Jeschke and Kokko 2009). Some prominent models explain these patterns through trade-offs and coadaptations between the traits themselves and mortality rates (Promislow and Harvey 1990; Charnov 1991, 1993; Kozłowski and Weiner 1997; Harvey and Purvis 1999), often incorporating elements of metabolic scaling theory (Brown et al. 2004). For example, a species experiencing low mortality can live a long adult life. It can then be selected to mature at a later age and larger size, because larger size increases the energy available to allocate to reproduction. If offspring size increases with body size at a higher rate than reproductive potential (as it does in mammals), the result is fewer but larger (and potentially higher-quality) offspring (Stearns 1992; Charlesworth 1994).

Support for the fast-slow continuum has been reported in a variety of taxa, including mammals (Oli 2004; Bielby et al. 2007), birds (Sæther 1987; Bennett and Owens 2002), reptiles (Bauwens and Diaz-Uriarte 1997; Clobert et al. 1998), and vascular plants (Franco and Silvertown 1996; Salguero-Gómez 2017). Recently, studies have moved away from using single traits to represent speed of life history, as they may not accurately represent a species' position on the fast-slow continuum (Bielby et al. 2007). Instead, studies attempt to reduce dimensionality in large multivariate data sets and find evidence for the fast-slow continuum if life-history traits load strongly and in the expected direction onto a first principal component axis (Jeschke and Kokko 2009).

Across taxonomic groups the fast-slow continuum of life histories has been shown to vary considerably, with some traits not following the pattern expected from Stearns's (1992) full continuum (e.g., Bauwens and Diaz-Uriarte 1997; Jeschke and Kokko 2009; Mayhew 2016). The continuum is best exemplified by mammals on which Charnov (1991) based his model, although, even for mammals, variations of the continuum including additional dimensions show greater predictive power (Galliard et al. 1989; Bielby et al. 2007). Few studies have attempted to quantify to what extent different clades deviate from the idealized fast-slow continuum or from each

other. This lack of quantitative comparisons makes it difficult to understand the relevance to different taxa of theories based on mammalian trait covariation.

Compared with vertebrates and plants, there is a lack of understanding about the relevance of the fast-slow continuum for invertebrates, particularly insects, which make up more than half of all described species (Grimaldi and Engel 2005). That said, the fast-slow continuum has been shown to be general and versatile enough to explain variation in groups only distantly related to the mammals in which it was originally proposed. Much interspecific comparative work on insect life histories so far has concentrated on finding relationships between pairs of traits: for example, positive correlations between body size and fecundity (Honěk 1993) and between body size and longevity (Holm et al. 2016), or the trade-off between egg size and number (Berrigan 1991). Some studies have addressed multiple traits in specific subtaxa of insects: Blackburn (1991) described evidence of a fast-slow continuum in parasitoid Hymenoptera, although the set of patterns found was limited by comparison with vertebrate taxa (Mayhew 2016). Specifically, some relationships predicted by the fast-slow continuum—such as smaller eggs laid in high-fecundity species—were upheld, but not others—such as the relationship between body size and life span (Blackburn 1991). The application of multivariate methods, such as principal component analysis (PCA), was prevented by gaps in the data across species (Mayhew 2016). Advances in phylogenetically based imputation mean that it is now feasible to conduct multivariate analyses even with missing data (Goolsby et al. 2017).

Orthoptera (grasshoppers, katydids, crickets, and their kin) are an ideal insect group on which to assess patterns of covariation between life-history traits. They are the most diverse order of polyneopteran insects, containing more than 22,500 species (Grimaldi and Engel 2005). They have a worldwide distribution and are largely phytophagous, and are relatively well studied, both in life history and phylogeny, with some species considered important crop pests (Jago 1998). They are hemimetabolous insects; they lack complete metamorphosis and instead have successive molts through nymphal stages, which resemble the adult stage (Grimaldi and Engel 2005). Orthopterans are diverse with respect to their life histories, for example, spanning 4.5 orders of magnitude in body mass (Whitman 2008). As in other insect groups, to date there has been no multivariate analysis of life-history variation in Orthoptera.

Here we assess the extent to which orthopteran life histories follow a fast-slow continuum using a multivariate approach. We compile a data set of life-history traits for this ecologically important insect group and apply phylogenetic imputation techniques to compare the life histories of a broad taxonomic sample of species. We predict that if orthopterans exhibit a fast-slow continuum, then all traits will load onto a principal component with the following loadings: positive for

body size, offspring size, development time, adult life span; negative for clutch size, clutch frequency, generations per year. We make direct comparisons between life-history trait associations for Orthoptera and those from other taxonomic groups to quantify their similarity in multidimensional space. This allows us to visualize the extent to which life-history theories devised around one taxonomic group might also be successful in explaining variation in other groups. Should the fast-slow continuum be general to all organisms, then we would expect that across taxonomic groups the structure of variation (as indicated by dimensionality reduction techniques like PCA) should remain consistent.

Methods

Orthoptera Data Collection and Imputation

We compiled data from the literature on body length (mean, where available, of male and female, excluding ovipositor and antennae as they can substantially increase length and distort estimates of body size; mm), egg size (at widest/longest part of egg; mm), juvenile development time (duration from hatching to adult eclosion; days), adult life span (duration from adult eclosion to death; days), clutch size (no. eggs laid in a single pod/bout of laying), clutch frequency (no. pods/bouts of laying per year), and voltinism (or no. generations per year; semivoltine, univoltine, bivoltine, multivoltine, or variable across geographic range). Where sources reported different values for the same species, the mean was calculated. For some species that live less than 1 year, if lifetime fecundity and either clutch size or frequency was reported, the missing variable was calculated by dividing lifetime fecundity by the relevant variable for which data existed. Egg size was chosen as the measure of offspring size because it was most frequently reported, but to compare between taxonomic groups we also collected body length at first instar (i.e., after parental investment in the egg stage; app. A; apps. A, B are available online). Voltinism was coded quantitatively as 0.5 (generations per year) for semivoltine, univoltine was coded as 1, bivoltine was coded as 2, and multivoltine was coded conservatively as 3. For species where voltinism was variable, the mean of the relevant above scores was taken. Continuous variables were natural log transformed to fit the assumptions of normality in the PCA. The full data set contained 610 species but was very sparsely populated. All data have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.sb307mm>; Bakewell et al. 2019).

Exploring orthopteran life histories in multivariate space requires a data set containing complete cases for each species. Unfortunately, this would leave us with a very small and taxonomically unrepresentative data set. To fill in gaps in our data set, we used a phylogenetic imputation method in the package Rphylopars (Goolsby et al. 2017) in R (R Core Team

2017). The phylopars function estimates the evolutionary covariance between species using the existing data, a phylogeny, and a model of evolution. Ancestral states and missing data with variances are imputed as the best linear predictions, maximizing the log likelihood of the covariance patterns in the original data (Goolsby et al. 2017). We tested several alternative models of evolution and selected a model fitting lambda (app. A). To determine the sensitivity of any qualitative results to the amount of imputation in the data set, we first performed the analyses described below on a subset of data with zero unknown traits and then repeated the analyses in series, each time expanding the subset of data, allowing it to contain extra species with an additional unknown trait. This resulted in seven data sets with increasing coverage of taxa. For each data set, we imputed missing values using the Davis et al. (2018) phylogeny and a model fitting lambda. We then extracted the imputed trait values and their estimated variances. Using these imputed values and variances, we generated normal distributions for each trait in each species and randomly sampled from these distributions to create 10,000 versions of each data set.

Phylogenetic PCA of Orthoptera

To assess the extent to which orthopteran life histories conform to the fast-slow continuum, we conducted phylogenetic principal component analysis (pPCA; Revell 2009) across our distribution of data sets using custom code (available via Dryad) in R (R Core Team 2017) developed from the functions in the package phytools (Revell 2012). PCA represents multivariate data by creating composite variables, measured along new axes, from the original data. The first principal component axis (PC1) encompasses the greatest amount of variance in the data, and subsequent orthogonal axes explain the second, third, and so forth, greatest amounts of variance in the data (Jolliffe and Cadima 2016). In this way PCA can be used to reduce the dimensionality of the data set, as fewer axes, each influenced by different variables, can explain a large amount of variance in the underlying data. Standard PCA methods assume that the data set is composed of independent data points, which is not the case with species-level data as closely related species are likely to be more similar in phenotype to each other than to distant relatives. To account for this, pPCA instead uses phylogenetic covariance to calculate the PC axes (Revell 2009).

At each level of imputation, we calculated phylogenetic covariance matrices using the Davis et al. (2018) Orthoptera phylogeny for each of the 10,000 data sets containing samples generated from the imputed trait values and their variances. We conducted PCA on these covariance matrices and recorded the eigenvectors and eigenvalues for each run. PCA produces singular vectors with arbitrary signs (i.e., in each eigenvector, all signs could be switched from positive to negative or vice

versa and the interpretation would be identical), but since we used bootstrapping over many models, each calculated on slightly different data, the sign of the eigenvectors becomes important to compare models (Bro et al. 2008). We used the procedure of Bro et al. (2008) to resolve ambiguity in the signs of the singular vectors by comparing their signs to the individual data vectors that they represent and reversing them if necessary. This is achieved by examining the sign of the inner product of the singular vector and the individual data vectors (Bro et al. 2008). After correcting signs, we used a resampling procedure to produce bootstrapped median eigenvectors, randomly selecting with replacement 10,000 sets of eigenvectors and calculating the median over 1,000 bootstraps.

As proposed in other taxonomic groups (Jeschke and Kokko 2009), if life-history trait covariation in Orthoptera strictly follows the fast-slow continuum concept, then all life-history traits should load strongly and in the hypothesized direction onto the first PC of a multivariate data set, and subsequent axes should explain little additional variance. We retained PC axes according to the Guttman-Kaiser criterion, where the axes with an eigenvalue greater than the mean of all eigenvalues are interpreted (Jolliffe and Cadima 2016). To assess the consistency of PCs calculated from each subset of data with increasing levels of imputation, we used hierarchical clustering on the variable loadings of each PC axis, based on euclidean distances. If PC axes are consistent across analyses with varying levels of imputation, then hierarchical clustering should resolve them as a clear separate group.

We also use bivariate correlations on the raw nonimputed data to evaluate the robustness of our conclusions from the pPCA, testing for relationships between body length (our most common variable) and the other life-history traits. We used phylogenetic generalized least squares (PGLS) models (Pagel 1999; Freckleton et al. 2002) in the R package caper (Orme et al. 2013) to test for these relationships while accounting for the nonindependence of data due to shared ancestry. PGLS uses a maximum likelihood approach to estimate λ —a measure of phylogenetic signal, or how strongly phylogeny predicts the pattern of model residuals (Pagel 1999). Sample sizes are listed with the results.

Analyses across Taxonomic Groups

For analyses across taxonomic groups, we built a data set from existing large-scale life-history databases that contained traits comparable to the orthopteran life-history traits: for mammals (Jeschke and Kokko 2009; Capellini et al. 2015; Myhrvold et al. 2015), reptiles (Myhrvold et al. 2015; Allen et al. 2017), and birds (Lislevand et al. 2007; de Magalhães and Costa 2009; Jeschke and Kokko 2009; Myhrvold et al. 2015). We collected six life-history traits for species across the four clades, the full details of which are in appendix A, briefly: body size (mass), offspring size (mass at independence from par-

ent), development time (time from independence from adult until sexual maturity), adult (reproductive) life span, clutch size (no. eggs/offspring per clutch/litter), and clutch frequency (no. clutches/litters per year). Voltinism was not present in any of the source data sets, so it was excluded from our analysis. This data set contained 932 mammals, 430 reptiles, 136 birds, and between 8 (at 0 traits imputed) and 339 orthopteran species (at a maximum of six traits imputed per species). For phylogenetic analyses, we merged six existing phylogenies (Fritz et al. 2009; Jaffe et al. 2011; Oaks 2011; Jetz et al. 2012; Pyron et al. 2013; Davis et al. 2018); full details and internal node dates are in appendix A.

We first performed pPCA on the combined data sets of orthopterans, mammals, reptiles, and birds using our composite phylogeny in an attempt to explore patterns of covariation at a broad taxonomic scale. We then assessed how much variance in each of the groups' data could be explained by the PC axes of the other groups. Unfortunately, this is nontrivial in pPCA, since the scores for species are based on differences in trait values from an ancestral state (which will change with the addition of extra taxa). Therefore, we performed the analysis without phylogenetic correction, effectively assuming that the impact of phylogenetic nonindependence is similar in all four groups. We took each taxonomic group (mammals, birds, reptiles, and orthopterans) in turn to be the baseline group and then calculated the amount of variance explained in the other groups' data by the retained axes of the baseline group (see app. A). Each trait in the data for this baseline group was standardized to have a mean of 0 and a standard deviation of 1. We then scaled the data for the other groups using these same scaling attributes; that is, species from different taxonomic groups with the same trait values would have the same scaled values. Scaling within groups does not affect the variance overlap calculations, but it gives more realistic relative scores along the resulting axes.

Results

The Fast-Slow Continuum Hypothesis in Orthoptera

The presence of a fast-slow axis encompassing body size in the data is strongly suggested by the results of the bivariate PGLS analyses (table 1), which do not use any imputation. Body size is strongly positively associated with offspring size, development time, and adult life span, although it is not significantly associated with generations per year or clutch frequency. However, in contrast with the standard fast-slow expectations, larger body size is strongly associated with larger clutch size in Orthoptera.

Three PC axes, explaining 83.27%–95.61% of the variance, were extracted per analysis on subsets of the data containing a maximum of zero, one, two, three, or four missing values per species (table B1; tables A1, B1–B3 are available online).

Table 1: Phylogenetic generalized least squares models of natural-logged body length against a series of (natural-logged) life-history traits from Orthoptera data as the response variable

Trait	$\beta \pm SE$	t	P	λ	n	R^2
Offspring size	.359 \pm .036	10.083	<.001	.964	159	.389
Development time	.425 \pm .155	2.741	.008	.768	82	.074
Adult life span	1.102 \pm .293	3.765	<.001	.000	29	.320
Clutch size	1.452 \pm .169	8.618	<.001	.919	110	.402
Clutch frequency	-.197 \pm .329	-.598	.565	.000	28	.014
Generations per year	.270 \pm .143	1.893	.062	.602	92	.028

Hierarchical clustering revealed consistency among some of these axes, with one axis (PC2 for 0 or 1 imputed value subsets, PC1 for the others; table B1) from each subset forming a distinct group with characteristics of a fast-slow continuum (fig. B1, available online), matching the PGLS results above. Table 2 shows the results of pPCA on the subset of data with maximum four imputed values, which is fairly typical of the others (table B1). In this case, PC1 is the fast-slow axis, with positive loadings of body size, offspring size, adult life span, and clutch size (fig. 1). The axis explains 41.40% of variance in the data, and increasing values indicate species with larger adult body size, larger eggs, longer adult lives, and more eggs per clutch (table 2).

Other axes retained at each level of imputation appear to be more sensitive to imputation, as they change more according to the amount of missing data and do not sit together under hierarchical clustering (fig. B1). However, with caution, other patterns may be interpreted. PC2 (table 2) is strongly loaded by clutch frequency alone. Clutch frequency is also a primary contributor to the axes retained in analyses at lower levels of imputation (table B1). The bivariate relationship between body length and clutch frequency was not significant and had zero phylogenetic signal (table 1).

The Fast-Slow Continuum across Taxonomic Groups

Only the first axis of the phylogenetic PCA across Orthoptera, Mammalia, Reptilia, and Aves was retained according to the Guttman-Kaiser criterion, regardless of the amount of

imputed data included for orthopterans. These first PC axes explained 67.0%–70.1% of variance in the combined data set (table 3, column “All (pPCA), PC1”; table B2). The axis was heavily loaded by adult body mass, offspring mass, development time, and adult life span, but not clutch size or frequency. These associations were found to be robust to the amount of imputed orthopteran data included in the analyses. Increasing values of PC1 here represent species with larger body masses and offspring at independence and longer developmental and adult/reproductive periods (table 3, column “All (pPCA), PC1”). The vertebrate clades cluster much closer to each other than to Orthoptera, which have the fastest life-history traits of the groups being compared, and of the three vertebrate groups, reptiles showed the most overlap in scores with orthopterans (fig. 2).

When computing life-history PCs for each group separately, in the vertebrate clades only PC1 was retained according to the Guttman-Kaiser criterion, while in Orthoptera the first two axes were retained (which combined explained 70.8%–89.2% of variation in the orthopteran data; table B3). The loading of traits was broadly similar across groups; the main differences occurred with fecundity-related traits. Specifically, in mammals and birds, clutch size loaded in the opposite direction to body size, offspring size, development time, and adult life span, while in reptiles and orthopterans it loaded in the same direction (table 3). When other groups’ life-history data were projected onto the axis of each individual group, the mammal and bird axes best explained variance in each other, performing poorer for reptiles and orthopterans (tables 3, B3).

Table 2: Bootstrapped median loadings from a phylogenetic principal component analysis (PCA) of orthopteran life-history data, imputed with a maximum four missing values per species (results of analyses at other levels of imputation can be found in table B1)

Trait	PC1 (95% CIs)	PC2 (95% CIs)	PC3 (95% CIs)
Body size	.763 (.762 to .764)	.135 (.129 to .141)	.011 (.006 to .016)
Offspring size	.514 (.513 to .516)	.048 (.044 to .053)	.002 (.000 to .005)
Development time	.223 (.220 to .226)	-.036 (-.041 to -.031)	-.110 (-.127 to -.089)
Adult life span	.922 (.921 to .922)	-.002 (-.006 to .002)	-.255 (-.262 to -.245)
Clutch size	.646 (.644 to .649)	.310 (.298 to .322)	.428 (.407 to .446)
Clutch frequency	.268 (.262 to .275)	-. .833 (-.839 to -.828)	.084 (.065 to .103)
Generations per year	-.197 (-.200 to -.194)	.075 (.068 to .083)	.350 (.327 to .368)
% variance	41.40	24.79	17.08

Note: Boldface indicates that the trait was significantly loaded onto the axis. CI = confidence interval.

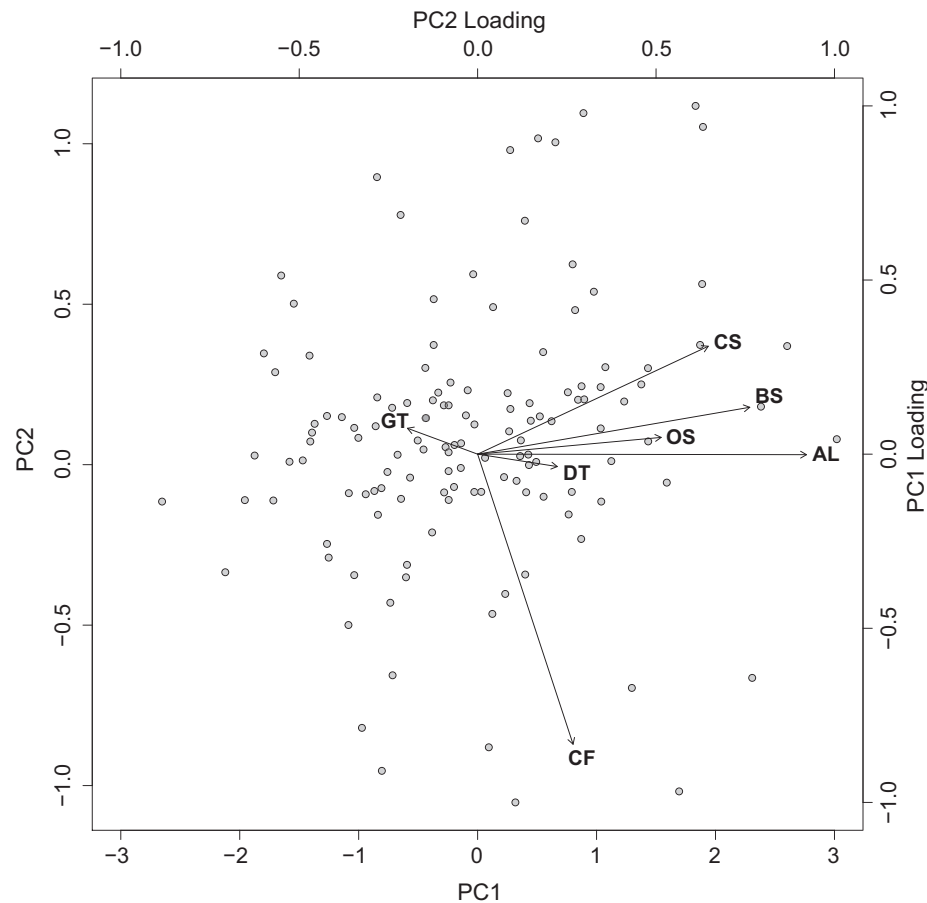


Figure 1: Biplot from the principal component analysis (PCA) of orthopteran life histories (table 2), which was produced using the imputed orthopteran data with a maximum of four missing traits. AL = adult life span; BS = body size; CF = clutch frequency; CS = clutch size; DT = development time; GT = generation time; OS = offspring size.

The reptile axes better explained variance in Orthoptera than any of the other groups, and vice versa (table 3; fig. 3; table B3).

Clutch frequency did not significantly load onto PC1 in any of the groups, but in Orthoptera, regardless of the amount of imputation used in the analysis, it is very heavily loaded onto the second axis. All three vertebrate clades scored similarly to Orthoptera in the amount of variance explained by this axis, although this is not surprising considering that it was largely influenced by a single trait. Figure 3 shows the distribution of species' scores along the axes proposed here for Orthoptera (table 3, column "Orthoptera").

Discussion

Understanding the causes of differences between species is a fundamental question in biology, and life-history traits represent some of the most prominent and important sources of phenotypic diversity (Stearns 1992; Charnov 1993; Roff 2002). Theories and paradigms that can be applied to multiple life-

history traits (e.g., Charnov 1991; Kozłowski and Weiner 1997) have the potential to explain this diversity, but the extent to which each one can depends on the extent to which associations between traits across organisms in general are similar (Jeschke and Kokko 2009). Problematically, attempts to quantify invertebrate life histories in multivariate space have been hindered by incomplete trait data (Mayhew 2016). Here we have used phylogenetic imputation methods to generate complete data sets of seven key life-history traits for a large number of Orthoptera species and used these to test associations between traits and find similarities across taxa. Without imputation, or with low-to-moderate levels of imputation, we find consistent evidence in our results of a fast-slow continuum axis. This axis is supported by bivariate PGLS analyses that consider only real (nonimputed) data. On these axes, we find evidence for some but not all of the relationships predicted by the fast-slow continuum. Moreover, we find that orthopteran trait variation resembles that of reptiles better than that of birds or mammals. Below, we put these findings

Table 3: Principal component analysis (PCA) of life-history traits between and within taxonomic groups and the amount of variance that each set of axes explains for each group

Trait	All (pPCA), ^a PC1	Mammal, PC1	Bird, PC1	Reptile, PC1	Orthoptera	
					PC1	PC2
Body size	.976	.431	.457	.484	.531	.160
Offspring size	.942	.444	.460	.471	.463	-.020
Development time	.418	.412	.451	.420	.297	.057
Adult life span	.490	.409	.362	.393	.510	-.257
Clutch size	.161	-.364	-.369	.370	.390	.346
Clutch frequency	-.213	-.384	-.330	-.276	.105	-.886
% variance mammals	67.8	69.9	69.4	40.7	29.4	10.4
% variance birds	67.8	69.5	70.0	40.8	31.5	11.6
% variance reptiles	67.8	37.1	37.1	62.3	53.9	19.8
% variance orthopterans	67.8	25.1	26.0	46.1	51.8	19.0

^a $\lambda = 0.976$.

Note: The “All (pPCA), PC1” column shows the loadings from a phylogenetically controlled PCA incorporating data from across mammals, birds, reptiles, and orthopterans (variance explained = 60.2%). Subsequent columns show the loadings of standard PCAs on data from each of the listed groups, along with the percentage of variance explained in each taxonomic group by these axes. Boldface indicates a significant loading, or the amount of variance explained in the clade used to generate the loadings. Definitions of traits are provided in appendix A. Orthoptera data are included imputed at the level of maximum four traits per species missing; results for other levels of imputation can be found in table B2 (phylogenetic cross-clade PCAs) and table B3 (within Orthoptera PCAs).

in the context of other work and assess their significance for life-history theory and ecology.

In orthopterans, larger values along the fast-slow axis (table 2: PC1) indicate species with larger body lengths, larger egg lengths, longer adult life spans, and more eggs per clutch. These results largely conform to the fast-slow continuum hypothesis, except that “fast” species have smaller clutches than “slow” species. Previous intraspecific studies in insects, including orthopterans, showed that larger size is associated with higher, not lower, fecundity (Honěk 1993; Strum 2016). Since most orthopterans are “income breeders,” (they acquire and invest resources for reproduction during their adult stage; Branson 2008) there is no reason a priori to believe that their reproductive budgets are fixed. Being income breeders might help larger insects to acquire more resources for reproduction. Taxa, like insects, which sit more toward the fast end of a fast-slow continuum, might favor allocation more toward number than size of offspring for many reasons: for example, a lack of density-dependent population regulation (as in the original r/K selection theory), if offspring lifetime fitness does not strongly depend on initial offspring size (Smith and Fretwell 1974), or if habitats for offspring development are not limiting (Godfray 1994).

Our results show that a single fast-slow axis does not adequately reflect the variation in orthopteran life histories, something that has been acknowledged in previous analyses in other taxonomic groups. The fast-slow continuum also makes predictions about development time (longer in “slow” species) and the number of generations per year (fewer in “slow” species). We do not consistently find these patterns in our analyses, although development time is loaded in the predicted direction (tables 2, B1). Although not as consistently as the

fast-slow axis, we find evidence of a secondary axis describing the frequency of clutches (tables 2, B1), which is similar to results from other groups. Salguero-Gómez et al. (2016) found support for the fast-slow continuum in plants but with a second “reproductive strategy” axis further resolving variation in fecundity traits. Even in mammals, Bielby et al. (2007) concluded that the life-history data did not support the concept of a single fast-slow axis; instead, two axes were required—one describing the trade-off between offspring size and number and another reflecting the timing of reproductive events (longer interbirth intervals associated with slower development). Mayhew (2016) described the life-history associations of parasitoid Hymenoptera as a reduced fast-slow continuum, and similar conclusions can be drawn for fish, birds, reptiles, and plants where some but not all of the expected patterns are found (Franco and Silvertown 1996; Bauwens and Diaz-Uriarte 1997; Jeschke and Kokko 2009).

Despite this, in our analysis conducted at the highest taxonomic level, the pPCA across mammals, birds, reptiles, and orthopterans, we retained only one axis that explains 67.03%–70.05% of the variance (table 3, column “All pPCA, PC1”; table B2). The traits that are significantly loaded on this axis all fit the expectations of the fast-slow continuum: larger values indicate larger adult and offspring size, slower development, and a longer adult life span. Neither clutch size nor frequency were loaded onto this axis, which may reflect disparity in how these traits load at lower taxonomic levels. It is interesting that at this very broad taxonomic scale a single fast-slow axis can be resolved, and this result is robust to the amount of imputed orthopteran data included in the analysis (table B1). PCAs in the vertebrate groups also recover a single axis (table 3), although these do not necessarily contradict previous

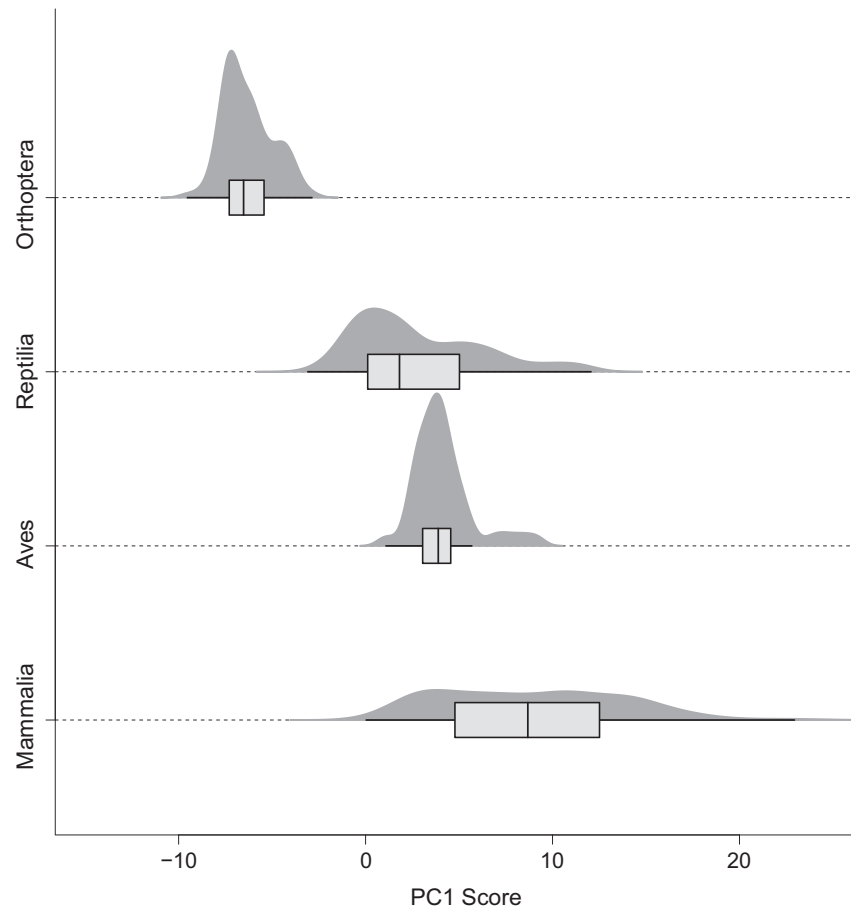


Figure 2: Distribution of species' scores on principal component 1 (PC1) of the phylogenetic principal component analysis of life histories across taxonomic groups (with Orthoptera data imputed with a maximum of four missing species: table 3). Boxplots show the median scores, quartiles, and 95% confidence limits.

findings such as those of Bielby et al. (2007) because of differences in the traits used between analyses.

Quantifying the fit of one taxonomic group to multidimensional axes of variation described by others could clarify the similarity in trait covariation across taxa. We showed that Orthoptera most closely follow the axes of trait covariation described by the reptiles (table 3), specifically resembling “fast” reptile species (figs. 2, 3). In the amount of variance reciprocally explained by their principal components, reptiles and orthopterans are more similar to each other than to mammals and birds (tables 3, B3), although the vertebrate clades cluster closer together in life-history trait space than reptiles do to orthopterans because of the disparity in body size (figs. 2, 3). The primary difference between orthopterans/reptiles and the other vertebrate clades is the loading of clutch size. Bauwens and Diaz-Uriarte (1997), in lacertid lizards, found that species with larger body sizes and offspring sizes also have larger clutches. These authors identify a trade-off between clutch size and frequency, which was negatively loaded

(although not significantly) compared with the other traits in our reptile PCA (table 3).

What might cause the similarity of trait covariation in reptiles and orthopterans? One possible driver is their body sizes, because as explained above, this might lead species toward the fast end of a fast-slow continuum to prioritize investment in number rather than size of offspring. Another obvious similarity is the range of possible clutch sizes. The range of clutch sizes in our data set is much smaller in mammals (with 20.1-fold variation across species) and birds (10.5-fold) than in reptiles and orthopterans (131- and 172-fold, respectively). Reptiles and orthopterans are ectothermic, while mammals and birds are endothermic. Ectotherms have lower metabolic rates than endotherms (White and Seymour 2003) and expend a much larger proportion of their metabolic energy on reproduction and early growth stages (Wieser 1985). Because of their lower metabolic power, endotherms may be more constrained in the timing of embryonic development and early growth, which have to be synchronized with external schedules

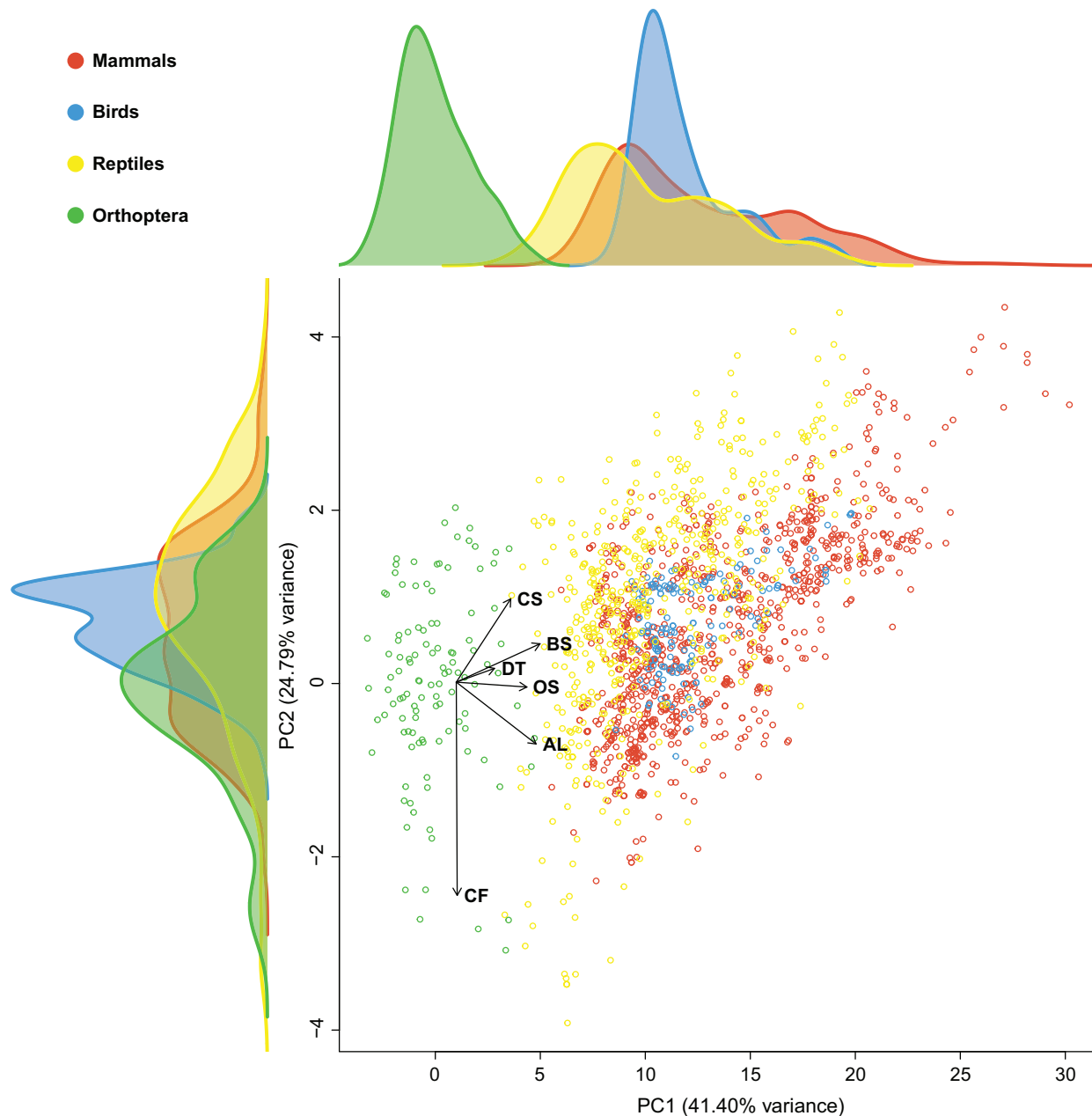


Figure 3: Biplot of principal component analysis (PCA) of orthopteran life histories (left, green), with mammals (right, red), birds (blue), and reptiles (yellow) projected into the same life-history space (table 3, column “Orthoptera”). Outer plots show the density of PC scores for each group. Arrows show the direction of trait loadings on these axes. AL = adult life span; BS = body size; CF = clutch frequency; CS = clutch size; DT = development time; OS = offspring size.

of environmental temperature (Wieser 1985). Accordingly, they will be more affected by factors such as seasonality and latitude, compared with endotherms. This may select for similar covariation in life histories. As outlined above, if lifetime offspring fitness is not strongly affected by initial offspring size, dividing the total resource pool allocated to reproduction between a greater number of offspring would result in higher

fitness (Smith and Fretwell 1974). Posthatching/birth parental care is extensive in birds and obligate via lactation in mammals, while in reptiles and orthopterans it is far less common (Clutton-Brock 1991). If in species with parental care individual offspring fitness is more dependent on their size, this may explain why orthopteran trait covariation is typically more similar to that of reptiles, particularly in the tendency for

larger-bodied species to lay larger rather than smaller clutches. Indeed, Gilbert and Manica (2010) show that in insects that with no parental care (or care limited to low-cost egg guarding) larger species produce more and larger eggs, while in those that provision offspring (similarly to birds and mammals) larger species produce fewer, larger eggs.

Multivariate studies of invertebrate life histories of the type conducted here are rare because in PCA species with data omissions are excluded, and trait data are typically incomplete across broad taxonomic groupings of invertebrates. However, without multivariate studies, it is difficult to assess how similar life-history trait covariation is across taxa and hence how powerful explanatory paradigms might be. Similarly, without such studies on invertebrates, which comprise the vast majority of described species richness, it is hard to assess how broadly relevant any theory or paradigm might be to biodiversity. Here we used recent methods of phylogenetic imputation to create a rich data set in a higher taxon of insects that is suitable for multivariate analysis. Although such methods have been tested in a limited way before and been found to be generally robust, our study has applied them in a data set that is more incomplete than usual. Skepticism about the imputed values is both healthy and legitimate, and it was incumbent upon us to demonstrate the robustness of findings based on them. We have done this in three ways. First, the associations between pairs of traits were first tested by analyses of data sets without imputed values—and these agree with those based on PCAs of imputed data (table 1). Second, the uncertainty in imputed values has been incorporated into our analyses by bootstrapping the imputed data and rerunning the multivariate analyses. We find very little variation in the results. Third, we reran our models with restricted data sets requiring less imputation and are able to identify consistency in the results by employing hierarchical clustering (fig. B1, tables B1–B3). This potentially opens up the possibility of many more such analyses on other taxonomic groups with incomplete data sets. However, the robustness of the findings to uncertainty in the imputed data should be addressed in each specific case.

The aim of life-history theory is to encompass a set of realistic evolutionary assumptions that allow the observed patterns of trait associations and values to be predicted. Based on previous work in other taxa, these assumptions might include growth rates and their scaling with temperature and body size, apportionment of energy to reproduction in the adult stage, and extrinsic and intrinsically imposed mortality rates (Charnov 1991, 2001, 2004; Kozłowski and Weiner 1997). Although there are doubtless some data on these variables already in the published literature for Orthoptera and other insects and invertebrates, particularly on pest or other model species, there has yet to be a concerted effort to compile these data as has been done in some vertebrate or plant groups (e.g., Jones et al. 2009; Salguero-Gómez et al. 2015, 2016).

Previous studies on other taxonomic groups have found that multivariate axes of life-history variation can help predict other ecological and community traits, which is not surprising given their impact on fitness and demography (Grime and Pierce 2012; Allen et al. 2017). Based on findings in other taxa, we expect that the axes identified for Orthoptera might predict the invasiveness of species or their pest status, conservation status, and spatial distribution in different habitats. Given the extensive ecological and economic impact of insects and other invertebrates in natural ecosystems, realizing this potential would have enormous practical application. However, the idea that life histories can be classified along a single axis applicable to all organisms is ambitious, and our results demonstrate the limitations of such a framework. Life-history evolution is addressed by many diverse hypotheses with different predictions; bet hedging, for example, predicts that with increased environmental stochasticity, organisms should favor variable development (e.g., through egg diapause in insects) and iteroparity (Evans and Dennehy 2005; Wilbur and Rudolf 2006). Without proxies of environmental uncertainty, however, it is hard to interpret the results of our analyses in this context. Ordination of life histories with ecological traits may be able to uncover more interesting and ecologically relevant patterns of association. In flying insects, using geometrid moths as an example, Davis et al. (2016) classified species along an axis following the degree of capital breeding (proportion of adult-acquired resources devoted to reproduction) and found correlates of this axis with larval diet breadth, reproductive season, and sexual size dimorphism.

To conclude, we have used phylogenetic imputation to conduct multivariate analyses of life histories in an insect group and found evidence of a fast-slow continuum, although one that is not as marked as in mammals and birds since clutch size loads in the opposite direction to body size. We demonstrate that in terms of both absolute trait values, and in their trait covariation, orthopterans resemble reptiles more than birds and mammals. These findings suggest that we need new theories to help us understand the reasons for these differences and similarities across taxa and investigations to understand their ecological consequences. They furthermore suggest that similar studies in invertebrate groups will be enlightening.

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Statement of authorship: A.T.B., P.J.M., R.P.F., and N.J.B.I. designed the study; A.T.B. designed the data-collection protocols, collected the data, and conducted the analyses; K.E.D.

created the expanded orthopteran phylogeny; A.T.B. and P.J.M. wrote the manuscript; and all authors revised the manuscript. P.J.M. supervised all stages of the research.

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