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Comparative analysis of behavioural traits in insects

Peter J Mayhew

Comparative studies of insect behaviour based on evolutionary trees are currently blossoming, because of the increasing ease of phylogeny estimation, the availability of new trait data to analyze, and a vast and growing array of statistical techniques for exploring data and testing hypotheses. These studies address not only the selective forces and constraints on insect behaviour, which are the realm of traditional behavioural ecology, but also their ecological and evolutionary consequences. Recent studies have significantly increased our understanding of foraging behaviour, interspecific interactions, locomotion and dispersal, communication and signalling, mate choice and sexual selection, parental care and the evolution of sociality. The curating of trait data remains a significant challenge to maximize the future potential of insect comparative studies.

Address
Department of Biology, University of York, Heslington, York YO10 5DD, UK

Corresponding author: Mayhew, Peter J (peter.mayhew@york.ac.uk)

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Introduction

Comparative analyses take variation across taxa as a source of data with which to test hypotheses [1,2] (Figure 1). Such tests often draw together large numbers of observations to provide a more holistic picture than studies on individual species can, and they relate to real-world situations (the data are often traits observable in the field), which is not necessarily true of experimental studies. Cross taxonomic data are also often readily available, and can show much wider variation than is obtained from single species or experimental studies. For these reasons they have wide appeal. The main limitations of comparative studies are that they are observational and often correlative in nature, hence cannot so robustly inform causation, and they are mostly limited to existing variation, which experimental studies are not. However, comparative analyses and experimental studies do overlap in the form of meta-analyses, where the results of many experimental studies, often involving several species, can be brought together to give holistic experimental tests of hypotheses [3•,4•].

Because cross-taxonomic variation potentially has an evolutionary basis, and the hypotheses that are tested are frequently explicitly evolutionary in nature, this brings analytical challenges that were first widely formalized in the 1980s, coincident with the development of computational methods for reconstructing phylogenies. It was then recognized that phylogenies themselves can help overcome those challenges [1]. In those days, phylogeny-based comparative approaches were often presented as ways to avoid falling into naïve statistical traps (such as treating species as independent data points), but more recently, since the development of likelihood-based and Bayesian computational techniques, along with information theoretic approaches, the emphasis has been on finding appropriate evolutionary models that explain the data well [2]. Techniques have diversified to incorporate an increasingly sophisticated range of data types and approaches (Table 1), although these can mostly be reduced to a small number of basic tasks, such as reconstructing of ancestral states and detecting evolutionary associations between traits (Figure 1, Table 1). To apply these techniques, a well resolved, and preferably dated, phylogeny is often essential [2].

In the past, and still to some extent today [5], phylogenetic requirements could present an obstacle for comparative studies, especially of insects. However, good quality phylogenetic information for insects is becoming more and more routinely produced thanks to widely available molecular markers [6,7], the development of whole genome and transcriptome approaches [8,9], and an increasingly better-known fossil record that provides the calibration points for dating analyses [10,11]. In addition to studies collecting primary morphological or molecular data, pipelines are now available that harvest existing molecular data from publically available databanks to produce trees [6,7,12], as well as compile existing phylogenies into larger meta-trees [13,14]. Large numbers of insect comparative studies now incorporate the development of bespoke phylogenies as an explicit step, and it is common for studies whose main output is a phylogeny to piggyback a comparative study as a selling point [15–17].

In addition to more trees on which to base studies, there are also more traits to analyze. Whole genomes and transcriptomes now allow us to investigate the evolution

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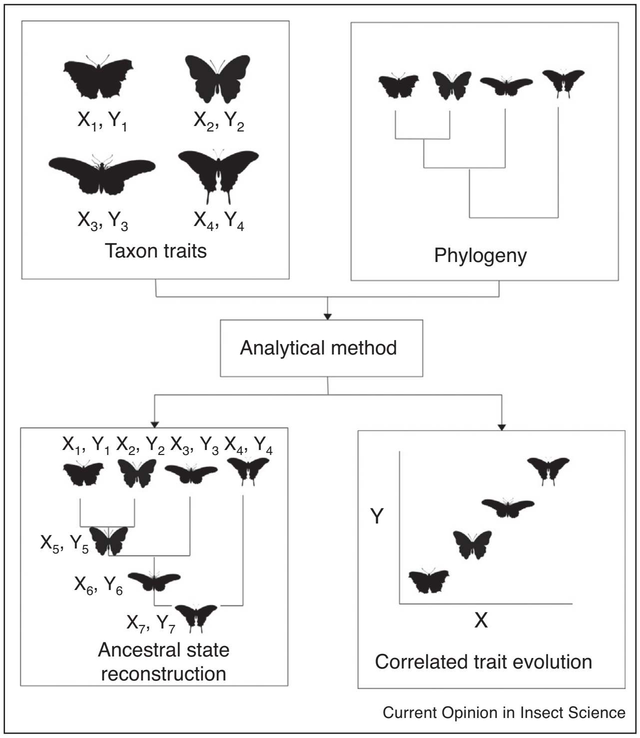
Figure 1



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A schematic diagram of the stages of a comparative analysis. Trait data are gathered across taxa (X and Y represent different traits, and the numeric subscripts indicate that each species is assigned a value for each trait from observation), and phylogenetic information assembled. This information is then integrated through one or more of a battery of analytical methods (Table 1) to produce a variety of outcomes (Table 1), the most common of which are ancestral state reconstruction (i.e. estimating the values of X and Y for ancestors of the living species for which we have data) and detecting evolutionary correlations between traits (i.e. whether evolutionary change in Y tends to be associated with evolutionary change in X).

of the genes that control phenotypic traits of interest [18•,19]. There has been a flowering of studies of macroevolutionary (speciation and extinction) rates, which can be inferred from the branching pattern on phylogenies [20–22,23••], or, in the case of extinction, from conservation designations [24]. From the perspective of behavioural traits, this means that we are better able to explore not only the causes of variation in behaviour across taxa (e.g. such as the selective pressures and constraints controlling them), but also their consequences (both ecological and evolutionary). Entomologists also study esoteric but fascinating questions, such as the function of halters in locomotion [25] and the choreography of silk spinning [26], which result from the unique variation in phenotypes produced by one of the world's most impressive adaptive radiations.

Here I collate recent comparative studies addressing the causes and consequences of variation in insect behavioural traits to illustrate the range of potential applications of comparative methods to such studies, and what they can tell us. I choose studies to illustrate a wide range of focal behaviours, although many studies illustrate well how these different categories of behaviour overlap and interact or influence each other [27••,28•,29,30•,31–33].

Recent comparative studies of behaviour

Foraging behaviour

Finding food, and a habitat that provides it, is necessary for all animals, and several recent studies have addressed how insects do this [3•,4•,34]. Patterns of host use in phytophagous insects are basis of terrestrial food webs, and may be shaped by experience, such that species are more likely to accept hosts they have previously encountered. Such conditioning may be adaptive if it facilitates decision-making in a complex community of potential hosts. Across 196 studies that had tested for this conditioning, such responses are indeed the norm, are just as common in monophagous as polyphagous species, and are just as likely to be produced by larval and adult experiences, but pupal experiences less so [3•]. Closely related species also show similar responses. Thus, previous conditioning likely exerts a powerful effect on realized patterns of host use in nature.

Other studies have addressed the consequences of foraging choices and habitat selection [20,22,23••,31,34,35]. For example, the phylogeny of skipper butterflies suggests that they fed ancestrally on dicot (broadleaved) plants, but some groups transitioned to monocot plants (grasses and allies) on which net diversification has been faster [22]. This is mainly attributable to two increases in net diversification rate within the monocot feeding clades which may have been triggered by climatic events which favoured the expansion of grasses first in forested, and then in more open habitats. This scenario suggests that behavioural (host choice) and abiotic forces (climate) have interacted to produce macroevolutionary effects mediated through the hosts, and intuitively this seems likely to be common in phytophagous insects.

Interspecific interactions

Recent comparative studies of predator-prey interactions have uncovered interesting associated trait variation [27••,32,36•]. In tiger moths and their relatives for example, hidden contrast colours (e.g. brightly coloured hindwings used to startle predators if crypsis fails) are more common in larger species [27••]. A theoretical model shows that contrast colours can evolve in larger species if larger species are easier for predators to detect when cryptic, and if larger signals can more effectively startle predators [27••]. Experiments with robotic moth models show that this is indeed the case.

The origin of some specialized trophic interactions, common in insects, is the focus of enduring interest [37,38].

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Table 1

Analytical methods applied by recent comparative studies of insect behaviour.

Method	Type of output	Computer applications	Recent studies
Ancestral state reconstruction with parsimony	A set of most parsimonious ancestral states	'Mesquite'	[35,43]
Bayesian ancestral state reconstruction	A set of most likely ancestral states and models of change	'RASP' [46]	[42]
Maximum likelihood ancestral state reconstruction	A set of most likely ancestral states for a given model of change	'ape' [47] and 'corHMM' [48] in *R*, 'Mesquite'	[35,40,41]
Reconstruction of ancestral biogeographic ranges	A set of most likely ancestral ranges and models of change	'BioGeoBEARS' in *R* [49], 'Lagrange' [50]	[43]
Blomberg's K estimate of phylogenetic similarity	Metric of phylogenetic similarity across species for a trait	'geiger' in *R* [51]	[26,33,52]
Sister-clade comparisons	Evolutionary associations between traits	N/A	[21,35]
Phylogenetically independent contrasts (PICs)	Evolutionary associations between traits	'caper' and 'ape' in *R* [47,53], 'Mesquite'	[19,26,41]
Lynch's phylogenetic mixed model [54]	Evolutionary associations between traits	'ape' in *R* [47]	[31]
Phylogenetic autoregression	Evolutionary associations between traits	'adephylo' in *R* [55]	[4•]
Pagel's discrete character association test [56]	Evolutionary associations between traits	'Mesquite'	[32]
Concentrated changes test for binary characters	Evolutionary associations between traits	'MacClade'	[32]
Bayesian modelling of trait evolution	Evolutionary associations between traits and transition rates between states	'BayesTraits' [57]	[5]
Generalized estimating equations [58]	Evolutionary associations between traits	'ape' in *R* [47]	[23••]
Phylogenetic ANOVA [59]	Evolutionary associations between traits	'phytools' in *R* [60]	[36•]
Phylogenetic Generalized Least Squares (PGLS) and Pagel's λ metric of phylogenetic constraint	Evolutionary associations between traits	'caper' in *R*	[24,27••,43,44•,61]
Phylogenetic Generalized Least Squares extended to incorporate measurement error	Evolutionary associations between traits, metric of phylogenetic constraint	Bespoke *R* script [34] based on [62]	[34]
Phylogenetic multivariate mixed models	Evolutionary associations between traits	'MCMCglmm' in *R* [43,63]	[3•,28•,39••]
Phylogenetic logistic regression [64]	Evolutionary associations between traits	'Phylolm' in R	[24]
Stochastic linear Ornstein–Uhlenbeck modelling	Evolutionary associations between traits	'SLOUCH' in *R* [65]	[20]
Ornstein–Uhlenbeck modelling of predator-regime specific dynamics	Model that best describes how predators affect evolution of a continuous trait	'OUwie' in *R* [66]	[40]
Phylogenetic principle component analysis	Reduction of multivariate cross-taxonomic data to principle components	'phytools' in *R* [60]	[26,36•]
Multivariate trait evolution modelling	Tempo and mode of evolution of multivariate traits	'MVmorph' in *R* [67]	[30•]
Bayesian analysis of speciation and extinction (BiSSE) [68]	Effect of a binary trait on speciation and extinction rates	'diversitree' in *R* [69]	[22]
Event-based analysis of co-phylogenetic structure	Type of events that best explain the co-phylogenetic structure	'Jane' [70]	[38]
Distance-based analysis of co-phylogenetic structure	Assessment of the congruence of two phylogenies	'Parafit' [71], 'PACo' [72]	[38]
Network analysis with approximate Bayesian computation	Rates of co-speciation and host shifting across phylogenies of interacting species	'abctools' in *R* [73]	[37]

A large data-base of global host records of phytophagous insects indicates that Lepidoptera which attack particular host orders are less likely use others (the main trade-off in host-use is between woody and non-woody plants, with insects being largely restricted to one of these groups but not both). These negative associations between host-use were mainly seen when comparing higher insect taxa, not closely related species, so the failure to detect host-use

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trade-offs in laboratory selection experiments does not necessarily mean they do not emerge over longer timescales. In Hemiptera, trade-offs in host use were not generally detected, so cannot explain host specialization in that group [39••]. The specificity of interspecific interactions such as these can also have wider ecological and evolutionary consequences [20,40]: a phylogeny of ambrosia beetles for example suggests that genera with broader host ranges tend to have diversified faster [20]. This might be because host switching facilitates reproductive isolation between incipient species.

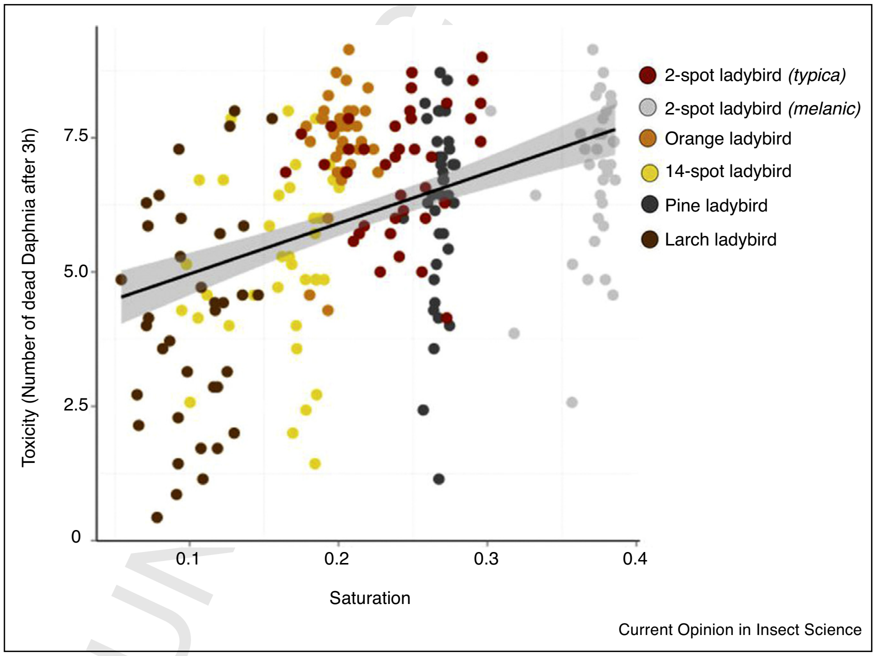
Dispersal and locomotion

Dispersal and locomotion ability are traits of ecological importance addressed by several recent studies [23••,24,41]. In the semi-aquatic bug group Gerromorpha, there is a variety of locomotion styles, from tripod-walking to rowing across the water surface (water striders). Phylogenetic reconstructions show that the ancestral habitat of the group was probably terrestrial or waterside vegetation, and a transition to living on the water surface was associated with an increase in locomotion speed across species, necessitated perhaps by increased predation risk and the need to move faster than the water when water is flowing, in order to maintain position. The increase in speed is correlated with the lengthening of legs and increasing body size, and adoption of a rowing action which decreases stroke rate, increasing efficiency [41]. The macroevolutionary consequences of locomotory and dispersal behaviour are also known to be far-reaching. In European butterflies, it is one of the life history traits that predicts a lower extinction risk, alongside high voltinism, and overwintering in later life history stages, presumably because it facilitates metapopulation persistence [24].

Communication and signalling

Explaining the diversity of animal signals is another enduring challenge to which recent comparative studies have contributed [29,33]. In ladybird beetles, for example, the wing cases (elytra) show a variety of colour patterns (often red or yellow against black), which are thought to warn predators of their toxicity. Comparing toxicity (determined experimentally) and colour patterns across several species, it can be shown that brighter colours are correlated with increased toxicity (Figure 2) suggesting that aposematic signalling is honest, implying evolutionary mechanisms which maintain this honesty.

Figure 2



Association between the colour intensity (i.e. saturation; how much colour there is compared to white light) of ladybird individuals belonging to different species, and the toxicity of those individuals as measured by their killing effect on *Daphnia* (linear mixed-effects model: $F_{1,54} = 5.57$, lower $p < 0.05$). Saturation is measured as the Euclidean distance between each colour and the achromatic centre of a cone-sensitivity weighted tetrahedral colour space. Briefly, the colour of each ladybird is plotted in four dimensions (tetrahedral space) where the four axes represent how much the four different cone cells of a bird are stimulated by the colour (standardized so 1 = full stimulation, 0 = no stimulation). Saturation measures the distance between the colour and the centre of the space representing white light, and the units are therefore standardized probabilities of absorption (for full details of the method see Figure 3 of [74]). The black line is a linear regression through the points (for indicative purposes only), and the grey area encompasses the regression standard errors.
Source: Reproduced from Figure 3 of [33] under the Creative Commons Attribution License (CC BY 4.0).

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A further experiment with model ladybirds showed that brighter colours are also more effective at deterring predators [33]. Fireflies are another group of beetles that show colour variety in their signals, this time produced by bioluminescence. Again, the signal is correlated with other species traits. Male fireflies that are active in early evening in vegetated habitats (when the background vegetation still reflects green) are predicted to produce light that contrasts better with the green background. This indeed is the case, as they tend to produce yellow light instead of green. Sedentary females and later active males however can use green light to their advantage in the dark to maximize reflectance from vegetation so their signals are more obvious, and their light is indeed greener [29].

Mate choice and sexual selection

Mate choice and sexual selection have produced impressive phenotypic variation addressed by comparative studies [18•,21,30•,42]. Male orchid bees attract females by perfumes which they construct by collecting volatile substances from orchid flowers, and which they store in specialized leg pouches. Traits like these that evolve by persistent strong sexual selection are predicted to evolve more rapidly than other traits. Mapping perfume traits across a phylogeny of 65 species, perfume chemistry was shown to display faster rates of evolution and a higher disparity compared to non-signalling traits, matching theoretical expectations. The complexity of the perfume increased with the number of sympatric congeners, suggesting that other species are one selective agent increasing signal diversity [30•]. Such sexually selected signals have also long been suspected to increase diversification rates. Recent evidence from insect and other animal species showing bioluminescent displays is consistent with this: those using lights in their courtship displays are more species rich than their relatives without these displays, but this is not true for non-courtship displays, suggesting that sexual selection indeed promotes species richness [21].

Parental care

Compared to birds and mammals, insects are not widely known for their parental care, but it is found in hundreds of species in many different taxonomic groups. The selective pressures that lead to care in one or either sex may depend on the ancestral states from which different types of care evolved. Across a dataset of over 2000 insect species, the ancestral care state was found to be no-care, and female-only-care was the most common type of care, evolving directly from no care, and sometimes transitioning to biparental care. Male-only-care also evolved from no-care in Hemimetabola, although quite rarely, whilst in a few cases biparental care evolved directly from no-care [5] (Figure 3). These findings are very different to those in vertebrates, where biparental care and male-only-care are more common, and female-only-care often evolves from biparental care. The lack of male care in insects may be the result of widespread sperm competition, which encourages males to desert and re-mate. The selective pressures favouring care have also been addressed in some studies: in acanthosomatine bugs maternal care is found in species which lack a protective covering for their eggs, suggesting that predation on offspring drives the evolution of care, and that there is a trade-off between different mechanisms of providing offspring protection [32].

Social evolution

Insect comparative studies have provided important evidence about the causes [43] and consequences [19,28•,44•] of sociality. *Polistes* paper wasps sometimes nest solitarily and sometimes cooperatively. Sheehan *et al.* [43] georeferenced data on nest foundress number worldwide, and then correlated it against climate data for those locations. They showed that cooperative nesting was more common in locations with short term instability in temperature, whilst the number of foundresses was lower in harsh environments. This suggests that cooperation is driven by selective responses to environmental conditions, but that the forces that regulate cooperation and foundress number may be different.

Kapheim *et al.* [19] compared the genomes of ten bee species with a variety of social structures to investigate the genetic mechanisms and consequences behind social evolution. They found that increasing social complexity (i.e. from solitary at one extreme to obligate complex eusociality at the other) was associated with increased capacity for gene regulation (more transcription factor binding sites in promotor regions, as well as the number of genes predicted to be methylated, which affects gene expression, and more rapid evolution of regulatory genes). Hence social evolution appears to have produced more complex gene networks.

Other behaviours

Entomologists often study more unique behaviours that do not fit easily into the standard pantheon of animal behavioural repertoires. Silk spinning, unknown in vertebrates, is widely used by spiders and insects to form structures (extended phenotypes) with obvious adaptive purposes, and likely macroevolutionary consequences [45]. One of the lesser known insect groups that does this is the Embioptera (webspinners), relatives of stick insects [8] which live in silk-lined burrows mainly in the tropics. The group is morphologically very uniform, but varies in silk-spinning behaviours, produced from modified forelimbs. By coding the movements of the legs and transitions between spin-steps and correlating them with other traits across a phylogeny, body size was shown to explain much of the diversity in spinning choreography across species [26], and there were also some differences between species inhabiting different microhabitats (such

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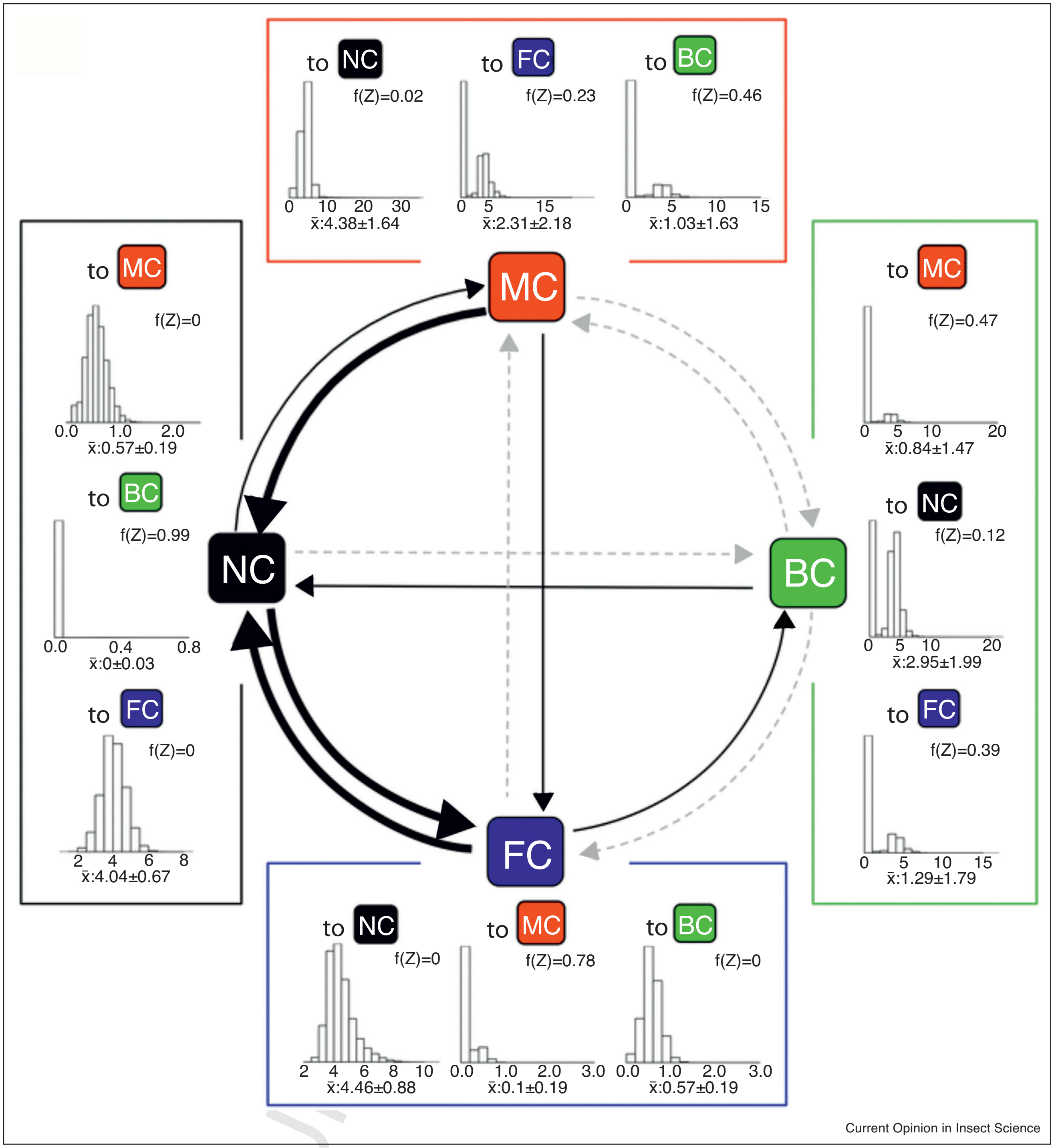
Figure 3



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Transition rates (events per unit branch length on the phylogeny) between parental care states, estimated from Bayesian analysis of phylogenies of hemimetabolous insects. *Abbreviations*: NC, no care; MC, male-only-care; FC, female-only-care; BP, biparental care. Histograms show the frequency distributions of rate estimates over the modelled posterior distribution. *f(Z)* = frequency at which the transition rate was zero. Arrow thickness is proportional to transition rates, and dotted lines are where the median rate ($\bar{x}$) ± standard deviations (given in the histograms) overlap zero. The highest transition rates are between no care and female-only-care (and vice versa), and also male-only-care to no care.
Source: Reproduced from Figure 4a of [5] under the Creative Commons Attribution License (CC BY).

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as tree trunks vs soil). Web spinning behaviours therefore seem to have evolved in concert with both transitions in microhabitat and morphology.

Conclusion

The insects contain the greatest adaptive radiations that can be seen with the naked eye [6,8,35]. There is arguably no greater resource to learn about the evolution of phenotypic diversity. To exploit it to the full we need to have access to phylogenies, trait data and analytical methods. Phylogenies and analytical techniques are much more accessible and useful to comparative biologists now than only a few years ago, but insect trait data still lie scattered across a vast heterogeneous landscape of natural history books, encyclopaedias, museum collections, scientific journals and other sources. To exploit the promise of insect comparative studies to the full, we need global digital data depositories that will collate, store and curate this information. Such trait-data hubs will finally bring comparative entomology fully into the information age.

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