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Comparative analysis of behavioural traits in insects

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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.

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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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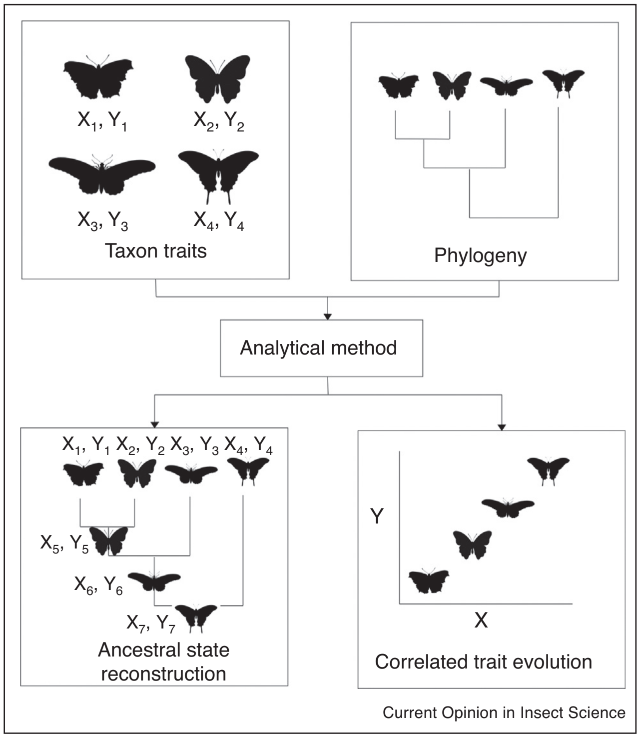
Figure 1



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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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