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Article:

Mayhew, Peter John orcid.org/0000-0002-7346-6560 (2018) Comparative analysis of behavioural traits in insects. *Current Opinion in Insect Science*. pp. 1-9.

<https://doi.org/10.1016/j.cois.2018.02.018>

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Manuscript Details

Manuscript number	COIS_2017_118_R2
Title	Comparative analysis of behavioral traits in insects
Short title	Comparative analysis of behavioural traits in insects
Article type	Review article

Abstract

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 analyse, 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 behavioral 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.

Corresponding Author	Peter Mayhew
Corresponding Author's Institution	University of York
Order of Authors	Peter Mayhew
Suggested reviewers	James Gilbert, Tom Sherratt

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Highlights

- Insect comparative studies help us to learn about the evolution of phenotypic diversity
- They use cross-taxonomic data, and require a phylogeny and analytical methods
- Trait data is still difficult to acquire and collate
- Phylogenetic data on insects have grown, as have analytical methods
- Recent studies have improved our understanding of the causes and consequences of all the major traits studied by behavioural ecologists

Comparative analysis of behavioural traits in insects

Peter J Mayhew

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

Tel: +44 (0)1904 328644

peter.mayhew@york.ac.uk

1 **Abstract**

2 Comparative studies of insect behaviour based on evolutionary trees are currently
3 blossoming, because of the increasing ease of phylogeny estimation, the availability
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9 interspecific interactions, locomotion and dispersal, communication and signalling,
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11 curating of trait data remains a significant challenge to maximize the future potential
12 of insect comparative studies.

13 **Introduction**

14 Comparative analyses take variation across taxa as a source of data with which to test
15 hypotheses [1,2] (Figure 1). Such tests often draw together large numbers of
16 observations to provide a more holistic picture than studies on individual species can,
17 and they relate to real-world situations (the data are often traits observable in the
18 field), which is not necessarily true of experimental studies. Cross taxonomic data are
19 also often readily available, and can show much wider variation than is obtained from
20 single species or experimental studies. For these reasons they have wide appeal. The
21 main limitations of comparative studies are that they are observational and often
22 correlative in nature, hence cannot so robustly inform causation, and they are mostly
23 limited to existing variation, which experimental studies are not. However,
24 comparative analyses and experimental studies do overlap in the form of meta-
25 analyses, where the results of many experimental studies, often involving several
26 species, can be brought together to give holistic experimental tests of hypotheses
27 [3,4].

28 Because cross-taxonomic variation potentially has an evolutionary basis, and
29 the hypotheses that are tested are frequently explicitly evolutionary in nature, this
30 brings analytical challenges that were first widely formalized in the 1980s, coincident
31 with the development of computational methods for reconstructing phylogenies. It
32 was then recognized that phylogenies themselves can help overcome those challenges
33 [1]. In those days, phylogeny-based comparative approaches were often presented as
34 ways to avoid falling into naïve statistical traps (such as treating species as
35 independent data points), but more recently, since the development of likelihood-
36 based and Bayesian computational techniques, along with information theoretic
37 approaches, the emphasis has been on finding appropriate evolutionary models that
38 explain the data well [2]. Techniques have diversified to incorporate an increasingly
39 sophisticated range of data types and approaches (Table 1), although these can mostly
40 be reduced to a small number of basic tasks, such as reconstructing of ancestral states
41 and detecting evolutionary associations between traits (Figure 1, Table 1). To apply
42 these techniques, a well resolved, and preferably dated, phylogeny is often essential
43 [2].

44 In the past, and still to some extent today [5], phylogenetic requirements could
45 present an obstacle for comparative studies, especially of insects. However, good

46 quality phylogenetic information for insects is becoming more and more routinely
47 produced thanks to widely available molecular markers [6,7], the development of
48 whole genome and transcriptome approaches [8,9], and an increasingly better-known
49 fossil record that provides the calibration points for dating analyses [10,11]. In
50 addition to studies collecting primary morphological or molecular data, pipelines are
51 now available that harvest existing molecular data from publically available databanks
52 to produce trees [6,7,12], as well as compile existing phylogenies into larger meta-
53 trees [13,14]. Large numbers of insect comparative studies now incorporate the
54 development of bespoke phylogenies as an explicit step, and it is common for studies
55 whose main output is a phylogeny to piggyback a comparative study as a selling point
56 [15-17].

57 In addition to more trees on which to base studies, there are also more traits to
58 analyze. Whole genomes and transcriptomes now allow us to investigate the evolution
59 of the genes that control phenotypic traits of interest [18,19]. There has been a
60 flowering of studies of macroevolutionary (speciation and extinction) rates, which can
61 be inferred from the branching pattern on phylogenies [20-23], or, in the case of
62 extinction, from conservation designations [24]. From the perspective of behavioural
63 traits, this means that we are better able to explore not only the causes of variation in
64 behaviour across taxa (e.g. such as the selective pressures and constraints controlling
65 them), but also their consequences (both ecological and evolutionary). Entomologists
66 also study esoteric but fascinating questions, such as the function of halteres in
67 locomotion [25] and the choreography of silk spinning [26], which result from the
68 unique variation in phenotypes produced by one of the world's most impressive
69 adaptive radiations.

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

76

77 **Recent comparative studies of behaviour**

78

79 Foraging behaviour

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

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

101

102 Interspecific interactions

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

110 The origin of some specialized trophic interactions, common in insects, is the
111 focus of enduring interest [37,38]. A large data-base of global host records of

112 phytophagous insects indicates that Lepidoptera which attack particular host orders
113 are less likely use others (the main trade-off in host-use is between woody and non-
114 woody plants, with insects being largely restricted to one of these groups but not
115 both). These negative associations between host-use were mainly seen when
116 comparing higher insect taxa, not closely related species, so the failure to detect host-
117 use trade-offs in laboratory selection experiments does not necessarily mean they do
118 not emerge over longer timescales. In Hemiptera, trade-offs in host use were not
119 generally detected, so cannot explain host specialization in that group [39]. The
120 specificity of interspecific interactions such as these can also have wider ecological
121 and evolutionary consequences [20,40]: a phylogeny of ambrosia beetles for example
122 suggests that genera with broader host ranges tend to have diversified faster [20]. This
123 might be because host switching facilitates reproductive isolation between incipient
124 species.

125

126 Dispersal and locomotion

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

141

142 Communication and signalling

143 Explaining the diversity of animal signals is another enduring challenge to which
144 recent comparative studies have contributed [29,33]. In ladybird beetles, for example,

145 the wing cases (elytra) show a variety of colour patterns (often red or yellow against
146 black), which are thought to warn predators of their toxicity. Comparing toxicity
147 (determined experimentally) and colour patterns across several species, it can be
148 shown that brighter colours are correlated with increased toxicity (Figure 2)
149 suggesting that aposematic signalling is honest, implying evolutionary mechanisms
150 which maintain this honesty. A further experiment with model ladybirds showed that
151 brighter colours are also more effective at deterring predators [33]. Fireflies are
152 another group of beetles that show colour variety in their signals, this time produced
153 by bioluminescence. Again, the signal is correlated with other species traits. Male
154 fireflies that are active in early evening in vegetated habitats (when the background
155 vegetation still reflects green) are predicted to produce light that contrasts better with
156 the green background. This indeed is the case, as they tend to produce yellow light
157 instead of green. Sedentary females and later active males however can use green
158 light to their advantage in the dark to maximize reflectance from vegetation so their
159 signals are more obvious, and their light is indeed greener [29].

160

161 Mate choice and sexual selection

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

177

178 Parental care

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

196

197 Social evolution

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

207 Kapheim et al. [19] compared the genomes of ten bee species with a variety of
208 social structures to investigate the genetic mechanisms and consequences behind
209 social evolution. They found that increasing social complexity (i.e. from solitary at
210 one extreme to obligate complex eusociality at the other) was associated with

211 increased capacity for gene regulation (more transcription factor binding sites in
212 promotor regions, as well as the number of genes predicted to be methylated, which
213 affects gene expression, and more rapid evolution of regulatory genes). Hence social
214 evolution appears to have produced more complex gene networks.

215

216 Other behaviours

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

231

232 **Conclusion**

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

244 Table 1. Analytical methods applied by recent comparative studies of insect
 245 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 <i>R</i> , 'Mesquite'	[35,40,41]
Reconstruction of ancestral biogeographic ranges	A set of most likely ancestral ranges and models of change	'BioGeoBEARS' in <i>R</i> [49], 'Lagrange' [50]	[43]
Blomberg's <i>K</i> estimate of phylogenetic similarity	Metric of phylogenetic similarity across species for a trait	'geiger' in <i>R</i> [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 <i>R</i> [47,53], 'Mesquite'	[19,26,41]
Lynch's phylogenetic mixed model [54]	Evolutionary associations between traits	'ape' in <i>R</i> [47]	[31]
Phylogenetic autoregression	Evolutionary associations between traits	'adephylo' in <i>R</i> [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 <i>R</i> [47]	[23]
Phylogenetic ANOVA [59]	Evolutionary associations	'phytools' in <i>R</i> [60]	[36]

Phylogenetic Generalized Least Squares (PGLS) and Pagel's λ metric of phylogenetic constraint	Evolutionary associations between traits	'caper' in <i>R</i>	[24,27,43,44,61]
Phylogenetic Generalized Least Squares extended to incorporate measurement error	Evolutionary associations between traits, metric of phylogenetic constraint	Bespoke <i>R</i> script [34] based on [62]	[34]
Phylogenetic multivariate mixed models	Evolutionary associations between traits	'MCMCglmm' in <i>R</i> [43,63]	[3,28,39]
Phylogenetic logistic regression [64]	Evolutionary associations between traits	'PhyloIm' in <i>R</i>	[24]
Stochastic linear Ornstein-Uhlenbeck modelling	Evolutionary associations between traits	'SLOUCH' in <i>R</i> [65]	[20]
Ornstein-Uhlenbeck modelling of predator-regime specific dynamics	Model that best describes how predators affect evolution of a continuous trait	'OUwie' in <i>R</i> [66]	[40]
Phylogenetic principle component analysis	Reduction of multivariate cross-taxonomic data to principle components	'phytools' in <i>R</i> [60]	[26,36]
Multivariate trait evolution modelling	Tempo and mode of evolution of multivariate traits	'MVMorph' in <i>R</i> [67]	[30]
Bayesian analysis of speciation and extinction (BiSSE) [68]	Effect of a binary trait on speciation and extinction rates	'diversitree' in <i>R</i> [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	'abctools' in <i>R</i> [73]	[37]

247 **Figure legends**

248

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

258

259 Figure 2. Association between the colour intensity (i.e. saturation; how much colour
260 there is compared to white light) of ladybird individuals belonging to different
261 species, and the toxicity of those individuals as measured by their killing effect on
262 *Daphnia* (linear mixed-effects model: $F_{1,54} = 5.57$, lower $p < 0.05$). Saturation is
263 measured as the Euclidean distance between each colour and the achromatic centre of
264 a cone-sensitivity weighted tetrahedral colour space. **Briefly, the colour of each**
265 **ladybird is plotted in four dimensions (tetrahedral space) where the four axes**
266 **represent how much the four different cone cells of a bird are stimulated by the colour**
267 **(standardized so 1 = full stimulation, 0 = no stimulation). Saturation measures the**
268 **distance between the colour and the centre of the space representing white light, and**
269 **the units are therefore standardized probabilities of absorption (for full details of the**
270 **method see Figure 3 of [74]).** The black line is a linear regression through the points
271 (for indicative purposes only), and the grey area encompasses the regression standard
272 errors. Reproduced from Figure 3 of [33] under the Creative Commons Attribution
273 License (CC BY 4.0).

274

275 Figure 3. Transition rates (events per unit branch length on the phylogeny) between
276 parental care states, estimated from Bayesian analysis of phylogenies of
277 hemimetabolous insects. NC = no care MC = male-only-care, FC = female-only-care,
278 and BP = biparental care. Histograms show the frequency distributions of rate
279 estimates over the modelled posterior distribution. $f(Z)$ = frequency at which the

280 transition rate was zero. Arrow thickness is proportional to transition rates, and dotted
281 lines are where the median rate $(\bar{x}) \pm$ standard deviations (given in the histograms)
282 overlap zero. The highest transition rates are between no care and female-only-care
283 (and *vice-versa*), and also male-only-care to no care. Reproduced from Figure 4a of
284 [5] under the Creative Commons Attribution License (CC BY).
285

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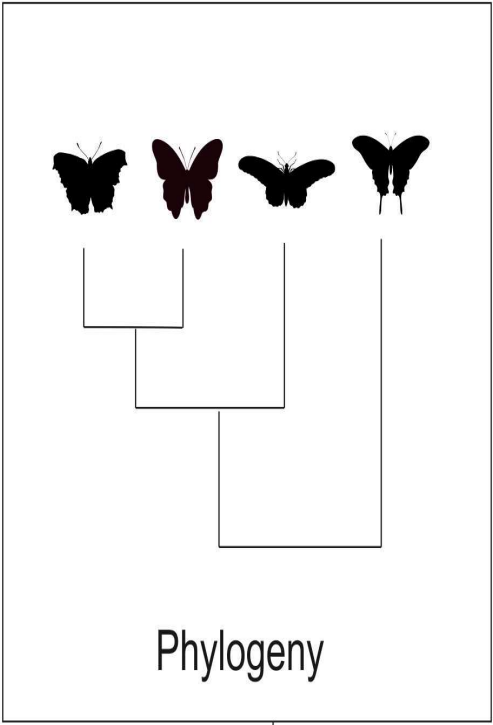
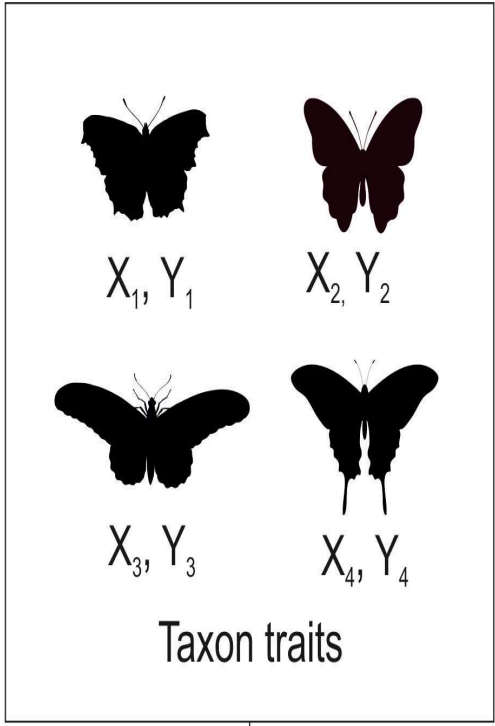
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Analytical method

