

to explain any additional choosiness beyond that necessary to maximize immediate fitness gains. The overwhelming importance of the direct benefits of female choice is indeed accepted for most mating systems. However, it would seem worthwhile to extend this approach to systems such as leks, where female choice is often pronounced, yet where many potential direct benefits of choice, such as mating with a fertile male or avoiding disease or harassment, have often been ignored<sup>7</sup>.

Evolutionary biologists are faced with many challenging opportunities for examining how female mating preferences have evolved. It may of course be that direct selection, good genes and runaway are all involved in the evolution of secondary sexual traits. However, demonstrating the relevance of any one process nevertheless requires exclusive supporting evidence. If our previous inability to resolve alternative models teaches us anything, it is perhaps that we should first consider the apparent exclusiveness of new tests thoroughly, before investing considerable effort in extensive research programmes that may only be capable of generating inevitably equivocal results.

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## Path Analyses of Selection

Joel G. Kingsolver and Douglas W. Schemske

*Identifying the targets and causal mechanisms of phenotypic selection in natural populations remains an important challenge for evolutionary biologists. Path analysis is a statistical modeling approach that may aid in meeting this challenge. We describe several types of path model that are relevant to the analysis of selection, and review some recent empirical studies that apply path models to issues in pollination biology, phenotypic integration and selection on morphometric and ontogenetic traits. Path analysis may play two roles in the analysis of selection: first, as an exploratory analysis suggesting possible targets of selection, which are then tested by direct experimentation; and second, as a means of evaluating the relative importance of different causal pathways of selection, once the likely targets of selection have been established.*

Which phenotypic traits experience selection in natural populations? What are the biological mechanisms underlying such selection? Despite a half-century of field studies in evolutionary biology, these central questions remain generally unanswered. The primary obstacle in field studies is the identification of the actual targets

and mechanisms of selection. These have been demonstrated convincingly in only a few cases<sup>1</sup>. The difficulty lies in distinguishing traits that are the actual targets of selection from correlated traits that do not experience direct selection. The multiple regression techniques championed by Lande, Arnold and Wade have greatly stimulated the analysis and measurement of selection on multiple phenotypic traits<sup>2–4</sup>, but these techniques have both statistical and biological limitations

for the identification of the actual traits under selection and for the examination of causal mechanisms<sup>1,5,6</sup>.

Several recent studies have proposed that the use of path analysis may help to address these problems. Path analysis has been used widely in population genetics, but is less familiar to most evolutionary ecologists interested in selection. When applied judiciously, path analysis holds considerable promise for the examination of mechanisms of selection on multiple phenotypic traits.

#### Path analysis and selection

Path analysis is a method for partitioning the correlations among variables. Sewall Wright<sup>7</sup> first developed path analysis as a means of interpreting quantitatively the causal relationships among a system of correlated variables. Wright<sup>8</sup> distinguished two distinct situations of special relevance to the analysis of selection: systems ordered in time, in which there may be a cause-and-effect relation be-

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tween 'earlier' and 'later' variables; and systems involving unmeasured, common factors.

Path analysis begins with the construction of a path diagram showing the relationships among all variables in the system (Box 1), based upon *a priori* knowledge of such relationships. In this sense, the path diagram represents a hypothesis for evaluation. The path coefficient indicates the direct contribution of one variable to the variation observed in another (see Box 1). Path analysis assumes that the relationships among variables are linear, so it is applicable only to the analysis of directional selection.

Because selection results from the covariation of phenotypic traits with relative fitness, applying the techniques of path analysis to selection is straightforward. For example, Lande and Arnold's<sup>2</sup> model of selection may be represented as a path diagram in which each phenotypic trait ( $X, Y, Z$ ) contributes directly to variation in fitness ( $W$ ) (Fig. 1a). Thus, in this simple case, the path coefficients directly represent selection, and these coefficients may be estimated by multiple regression analysis. An important advantage of Lande and Arnold's approach is that estimates of the selection coefficients (the selection gradient in Lande and Arnold's terminology) may be directly incorporated into models of phenotypic evolution<sup>2</sup>.

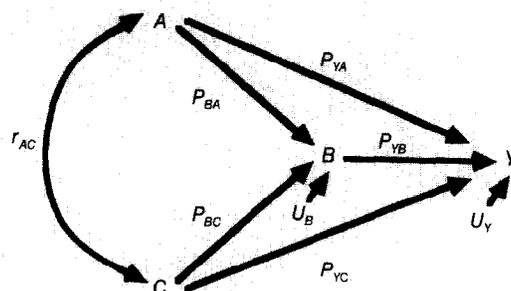
One way to represent causal mechanisms of selection is to incorporate in the path diagram intermediate variables that relate phenotypic traits to fitness (Fig. 1b). In this sense, selection on some trait  $X$  results from the effects of  $X$  on some intermediate variable  $P$  that in turn affects fitness  $W$ . As Arnold<sup>9</sup> noted, these relationships can be represented in a path diagram with direct paths from phenotypic traits through intermediate variables to fitness. Because of the equivalence of path coefficients and of selection coefficients in Lande and Arnold's model,  $P_{W/PX}$  may be interpreted as the selection coefficient for trait  $X$  via its effects on the intermediate variable  $P$  - i.e. selection via a specific causal path. Again, these path coefficients may be estimated by a series of multiple regressions (see Box 1).

**Box 1. Path analysis with measured variables**

Path analysis is a method for quantifying the relationships among variables based on an *a priori* model, the path diagram, that specifies the causal and noncausal paths between independent and dependent variables. Path analysis assumes that the relationships among variables are linear, that there is no correlation between residuals, that observed variables are measured without error, and that there is no reciprocal causation between variables<sup>20,21</sup>.

In the path diagram below, a straight, single-headed arrow between two variables reflects a causal relationship, while a curved, double-headed arrow reflects correlation without causation (e.g.  $r_{AC}$ ). For measured variables, path coefficients are standardized partial-regression coefficients, which may be obtained from a multiple regression on standardized variables for each dependent variable in the path diagram. For example, the path coefficient  $P_{YA}$  in the diagram below represents the direct effect of variable  $A$  on variable  $Y$  with all other variables held constant. An indirect effect is simply the product of the path coefficients representing multiple causal paths. The total correlation between independent and dependent variables can include causal contributions from direct and indirect effects, and noncausal contributions from spurious and unanalysed paths<sup>20</sup>. The sum of the direct and indirect effects is the effect coefficient, and represents the expected change in a given dependent variable due to change in one of its causal variables.

In the diagram, the paths  $AY, BY$  and  $CY$  represent the direct effects of the independent variables  $A, B$  and  $C$  on  $Y$ , and the paths  $ABY$  and  $ACY$  are the indirect effects of  $A$  and  $C$  on  $Y$ . All other paths contributing to the correlations observed between variables for this path diagram are noncausal, either because they include a double-headed arrow (an unanalysed contribution, e.g.  $YAC, BAC$ ), or because they include the effects of other causal variables (spurious contributions; e.g. the paths  $YAB$  and  $YCB$  are the spurious contributions to the correlation between  $Y$  and  $B$ ). The residual variables  $U_B$  and  $U_Y$  include all unmeasured variables that affect the dependent variables  $B$  and  $Y$ , respectively. The path coefficient for a given residual variable is calculated as  $\sqrt{1-R^2}$ , where  $R$  is the proportion of variation in the dependent variable that is explained by the model.



One approach to significance testing in path analysis is to determine how accurately the path diagram reproduces the actual correlation matrix<sup>20,21</sup>. Such analyses are restricted to overidentified path diagrams, where the number of equations available to solve for the parameters is greater than the number needed for parameter estimation. When maximum likelihood methods are used to estimate the coefficients, one can also test the difference between two alternative path diagrams with log-likelihood ratios<sup>22,23</sup>.

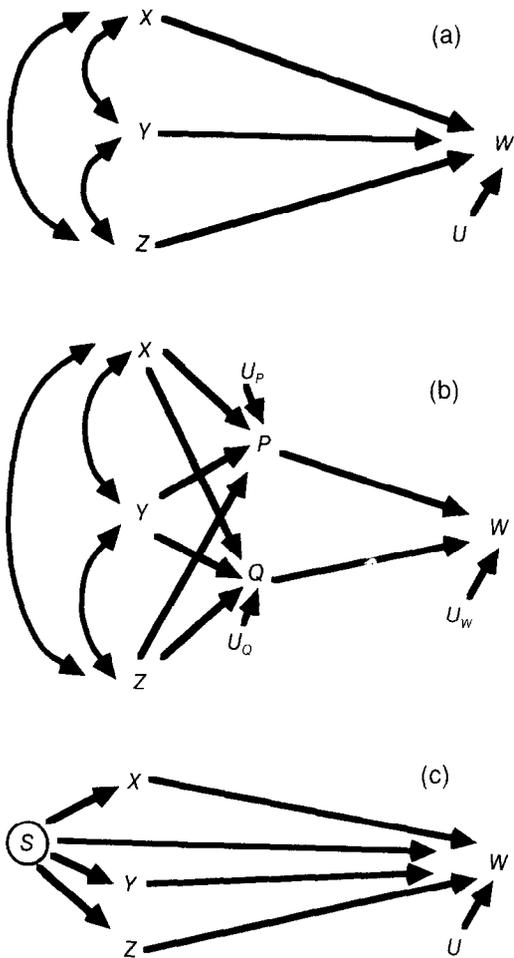
Significance testing of individual path coefficients is of dubious value for the development of the path diagram when indirect effects will also be estimated. As an example, imagine that in the diagram the path coefficient for the direct effect of  $A$  on  $Y$  ( $P_{YA}$ ) is 0.36, and that the path coefficients for the effect of  $A$  on  $B$  ( $P_{BA}$ ) and of  $B$  on  $Y$  ( $P_{YB}$ ) are each 0.60. The magnitudes of the direct and indirect effects for this system are identical (0.36), yet we may find that  $P_{YA}$  is not statistically significant, whereas  $P_{BA}$  and  $P_{YB}$  are significant. Deleting variable  $A$  from the path diagram by virtue of its insignificant direct contribution to the variation in  $Y$  ignores its substantial indirect effect on  $Y$ , and reduces the accuracy of the model.

An important difficulty in the analysis of selection is the existence of highly correlated phenotypic traits. For example, if selection actually acts on some unmeasured aspect of phenotype that is correlated with the measured variables, the interpretation of the selection coefficients obtained from regression analyses may be misleading<sup>5,6</sup>. In keeping with Wright's original application of path analysis, several workers<sup>6,10,11</sup> have used path models in which selection may act on unmeasured phenotypic factors, for which the measured traits are imperfect indicators (Fig. 1c). Here, the covariances among the measured variables are modeled in terms of one or more unmeasured factors, with the goal of identifying possible targets of selection that are

not measured directly in the system (see Box 2). For systems of morphological traits, relevant unmeasured factors might include overall size and shape allometry. The use of general factors may make the analysis more stable to the addition or omission of measured traits in the path diagram<sup>10-12</sup> (but see below). This is particularly relevant to systems with large numbers of correlated traits. One limitation of incorporating unmeasured factors into the path diagram is that the estimated selection (path) coefficients cannot be incorporated directly into existing models of phenotypic evolution.

**Case studies**

Several recent studies have used path analyses of the sort described



**Fig. 1.** Path diagrams for three models of phenotypic selection. See Box 1 for terminology. Here, X, Y, Z, P, and Q are measured phenotypic traits, W is fitness, S is an unmeasured phenotypic factor, and U is a residual variable. (a) Path diagram of the Lande–Arnold model of selection on traits X, Y and Z. (b) Path diagram illustrating selection on traits X, Y and Z via intermediate traits P and Q. (c) Path diagram of selection on traits X, Y and Z incorporating an unmeasured factor S.

in Fig. 1b, c. Here, we briefly review studies applying path analysis to issues in pollination biology, phenotypic integration and selection on size, shape and ontogeny.

*Pollination and plant reproductive success*

Studies in pollination biology have often hypothesized a relationship between pollinator visitation and plant floral characters. Pollination biologists have recently turned to path analysis to provide a way of estimating how pollinators may contribute to plant reproductive success<sup>13</sup>.

What is most desirable in studies of this kind is simultaneously to examine floral characters, pollinator visitation and plant success. Stanton and colleagues<sup>14</sup> estimated the contributions of floral characters, pollinator visitation and postpollination success to variation in seed paternity (a measure of a plant's

contribution to reproductive success through male function) in the mustard *Raphanus sativus*.

Path analysis revealed substantial variation among pollinators in their effects on seed paternity, and in the effects of floral characters on visitation (Fig. 2). Of the four pollinator groups, only small bees had a substantial positive contribution to variation in seed paternity, and honeybees had a large negative effect on seed paternity. The floral characters contributing most to higher visitation by honeybees were pollen-grain size and petal size, while pollen number had the largest positive effect on visitation by small bees. The direct contribution of pollen-grain number to seed paternity was small and negative, while the indirect effect, obtained by summing the products of the path coefficients for all indirect paths, was rather large and positive. These results indicate how path analysis can be used to reveal the complex relationships between phenotypic traits and reproductive success.

*Phenotypic integration and plant performance*

Physiological ecologists are interested in the ways that physiological, phenological and morphological traits contribute to overall performance, i.e. phenotypic integration. Path analysis – path diagrams concerning the pattern of phenotypic integration within a population – provides a way of testing various hypotheses.

Evans (PhD thesis, University of Chicago, 1990) used path analysis to determine the contribution of physiological, phenological and allocation traits to among-plant variation in growth and reproduction of *Brassica rapa* grown in three distinct nutrient environments (Fig. 3). She found that the direct effects of phenology and leaf physiology varied across treatments. For example, specific leaf weight had a positive effect on leaf biomass in all three treatments, but the magnitude of this effect decreased from the low to the high nutrient treatment. Indirect effects of phenological and physiological traits on reproductive biomass were often as large as the direct effects. For example, the indirect effect of specific leaf weight on

**Box 2. Path analysis with unmeasured common factors**

In factor analysis, the covariation among measured variables may result from their common dependence on some unmeasured factor or factors. Thus, for a set of morphometric characters the correlations among traits may be a consequence of their common dependence on factors of overall size or shape. The goal of path-analytic models of selection in terms of unmeasured factors is to identify possible targets of selection that may not be measured directly.

There are several approaches to estimating coefficients in such path models. Crespi and Bookstein's<sup>6,11</sup> analysis of morphometric traits for the case where fitness is a dichotomous variable (live or dead) has two steps. First, the overall size factor is defined in terms of the first within-group (i.e. within fitness classes) principal component (i.e. the first eigenvector) of the covariance matrix of the phenotypic traits. The coefficients of this eigenvector are then used to estimate a score for overall size for each individual. Second, analysis of covariance for each phenotypic trait is performed in order to examine the difference in mean trait value for live and dead groups after the trait is adjusted for overall size. The selection coefficient for a trait is then defined as the size-adjusted mean difference between the fitness groups. Note that this analysis assumes that the first within-group principal component can be interpreted as overall size<sup>24</sup>. If selection operates strongly on size, the amount of size variation within fitness classes may be relatively small, making this interpretation problematic.

An alternative approach to the estimation of path models, exemplified by LISREL (Linear Structural Relations models), uses the maximum likelihood of the covariance matrix to estimate all model parameters simultaneously<sup>22,23</sup>. One advantage of LISREL is that it facilitates significance testing of comparisons between alternative path models for a data set, using log-likelihood ratios. One difficulty with the LISREL approach is that it requires explicit specification of the nature of residuals and error terms in the model<sup>25</sup>; for most ecological and evolution studies these may be difficult or impossible to verify.

reproductive biomass in the medium treatment was nearly as large as the direct effect. Differences in the sign of direct and indirect effects were also observed. For example, the direct effect of specific leaf weight on reproductive biomass in the medium treatment was negative, whereas the indirect effect was positive. These results suggest that

the functional relationships among plant traits involve paths of causation that vary across environments.

In a similar study of functional integration, Farris and Lechowicz<sup>15</sup> developed a path model to investigate the factors affecting fruit production in the annual plant *Xanthium strumarium*. Their path model was not based on previous observations or on hypotheses regarding causal paths, but was instead derived from a series of multiple-regression analyses from which only the best predictor variables were used in the path analysis. This approach assures that the final path model will account for the greatest amount of variation in all dependent variables, but is unlikely to reveal the true functional relationships among traits.

*Selection on size and shape*

Morphological traits that reflect the size and shape of organisms have been identified as targets of selection in numerous studies<sup>1</sup>. Because these traits are often highly correlated due to the effects of overall size, it is often difficult to distinguish selection on a particular morphological trait from selection on size. In addition, the large correlations among size-related traits can result in estimated selection coefficients that are not robust to the addition or deletion of other traits to the analysis, especially when multiple regression is used to estimate selection<sup>7,10</sup>. One approach to these problems is to use factor analysis to compute a general size factor from the measured morphological variables<sup>6,11</sup> (Box 2). A path analysis is then constructed in which size and the size-adjusted morphological traits influence fitness.

Crespi and Bookstein<sup>6,11</sup> used a path analysis incorporating size as an unmeasured factor in a reanalysis of Bumpus<sup>16</sup> data on the survival of house sparrows (*Passer domesticus*) following a winter storm. Crespi and Bookstein estimated the directional selection coefficients on both the unmeasured size factor and on size-adjusted morphological traits. Analyses were conducted on both sexes for all nine traits measured by Bumpus, and on a subset of seven traits (total length and weight were excluded). For comparison, they also conducted a mul-

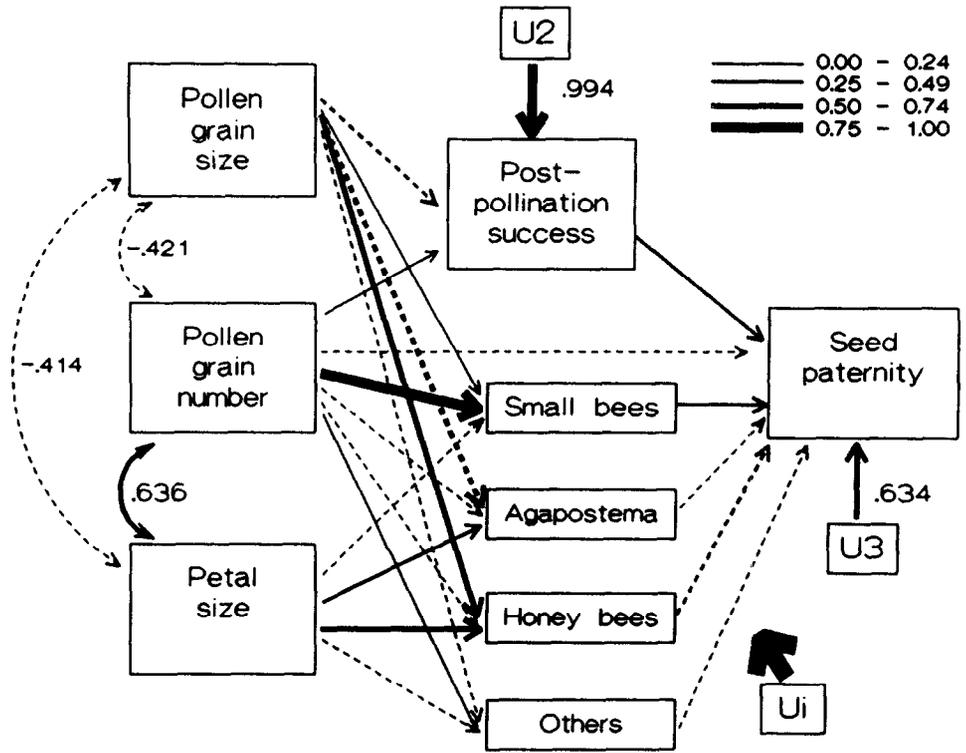


Fig. 2. Path diagram of the determinants of variation in seed paternity in *Raphanus sativa*. Floral characters (pollen grain size and number and petal size) can affect seed paternity via their effects on visitation rates by different pollinators (small bees, *Agapostema* bees, honeybees and other pollinators) and via their effects on post-pollination success. Here, solid lines indicate positive effects, and dashed lines indicate negative effects; the width of the line indicates the magnitude of the effect. From Ref. 14.

multiple regression analysis following the approach of Lande and Arnold<sup>2</sup>. If significant selection coefficients only are considered, the factor/path analysis and the multiple-regression analysis gave identical results for both sexes for both the seven- and nine-trait data sets. For the nine-trait data set, selection was observed on weight for females, and on total length and weight for males. For the seven-trait data set, no significant selection was detected for females, but selection was observed on wing length for males.

Crespi and Bookstein also performed multiple regression analysis and factor/path analysis on data sets of four and seven morphological traits obtained from pentatomid bugs. This allows one to evaluate whether the selection coefficients obtained from regression analysis are more sensitive (less robust) to the choice of characters<sup>6</sup>. For the four-trait data set, both analyses gave a significant selection coefficient for forewing length only. In the seven-trait data set, regression analysis indicated significant selection on two scutellum traits, but no selection on forewing length. In contrast, the factor/path analysis for this data set indicated significant selection on four characters, including forewing length and two traits that were not found to be significant by this analysis in the original four-trait

data set. It is clear that for these data, neither the regression nor the factor/path results are very robust to the addition of traits to the analysis.

*Selection and ontogeny*

Path analysis can also be useful for examining selection acting at different ontogenetic stages for traits that change through the life cycle<sup>17,18</sup>. Identifying those life stages that make the greatest direct or indirect contribution to variation in fitness is of particular interest.

Maddox and Antonovics<sup>10</sup> used a path analysis of determinants of fitness variation in two *Plantago* species. The number of leaves and the area of the median leaf, determined at each of five different developmental stages, were used as indicators of the unmeasured factor, total leaf area. Three reproductive factors were also estimated, and fitness was an unmeasured factor indicated by seed number and seed mass. The path diagram was based on the hypothesis that leaf area has a direct effect on fitness through seed filling, and an indirect effect through the formation of reproductive structures. They found that the model provided a marginally acceptable fit to the observed data, and that the path diagrams for the two species did not differ significantly. Stages in the middle of the life cycle made the greatest

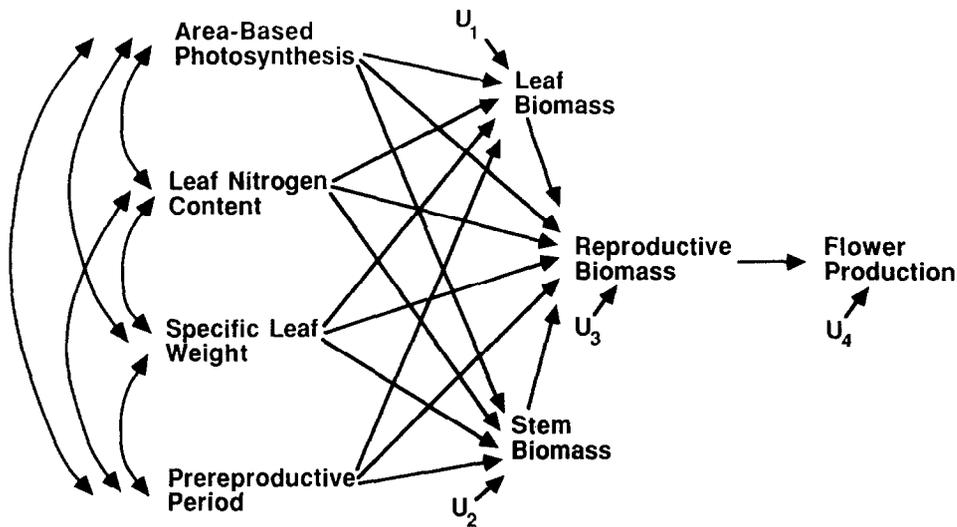


Fig. 3. Path diagram of the determinants of variation in allocation to reproduction (reproductive biomass and flower production) for *Brassica rapa*. Plants were grown in each of three different nitrogen environments, and a path analysis was performed for each treatment. Physiological and phenological traits (area-based photosynthetic rate, leaf nitrogen content, specific leaf weight and length of the prereproduction period) can affect reproductive biomass both directly and indirectly via effects on allocation to leaf and stem biomass. Based on Evans (PhD thesis, University of Chicago, 1990).

contribution to variation in seed production.

In a similar study, Mitchell-Olds and Bergelson<sup>19</sup> used path analysis to examine the effects of seed weight, germination date, plant size in June and early and late growth on final adult size in the annual plant *Impatiens capensis*. They found that early growth rate had the largest total causal effect on final adult size, with substantial positive contributions from both direct and indirect effects.

**Future prospects**

Path analysis is a method for partitioning the correlations among variables in the context of a specific hypothesis, the path diagram. It cannot replace more direct methods for identifying the targets or mechanisms of selection using experimental manipulations of phenotype or of the selective environment<sup>1,5</sup>. The uncritical application of path models to the analysis of selection in natural populations will be likely to yield misleading and erroneous results.

We suggest two possible roles that path models may play in the analysis of selection. First, as emphasized by Crespi and Bookstein<sup>6,11</sup>, path analysis may be used in an exploratory manner<sup>8</sup> to suggest traits that may be under direct selection. These suggestions can then be tested using more direct experimental methods<sup>1,5</sup>. Second, after the likely targets of selection are established, path models may be used to evaluate the relative importance of different causal path-

ways relating phenotypic variation to fitness variation. These applications of path analysis may add to our understanding of the targets and mechanisms of selection in natural populations.

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