Path Analysis: A Critical Evaluation Using Long-Term Experimental Data

Felisa A. Smith; James H. Brown; Thomas J. Valone

PATH ANALYSIS: A CRITICAL EVALUATION USING LONG-TERM EXPERIMENTAL DATA

FELISA A. SMITH,* JAMES H. BROWN, AND THOMAS J. VALONE†

Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131

Abstract.—We evaluated the ability of path analysis to characterize direct and indirect interactions in a natural ecological system. Based on previous experimental work, we constructed a path diagram reflecting presumed relationships between kangaroo rats (*Dipodomys* spp.) and two other small rodent species. The technique was applied to examine the direct effects of competition and indirect effects mediated through vegetation. Path analysis gave varying and sometimes uninterpretable results when applied to data collected from unmanipulated and manipulated systems. The variation most likely can be attributed to some combination of inadequate specification of the path diagram, differences between unmanipulated and manipulated systems, varying responses to experiments of different duration, and natural temporal variation. Because these issues are applicable to many kinds of complex systems, we suggest caution before applying and when interpreting the results of path analysis.

A major problem of contemporary science is to understand the structure and dynamics of complex systems. Many physical, biological, and social systems are composed of multiple interacting components. Examples include chemical reactions involving multiple reagents, neural networks (both real and artificial), and animal and human societies. Of particular interest to this audience are interactions among species in ecological communities, among genes in developmental pathways, and among traits in determining fitness. In such complex systems, it can be difficult to isolate causes and effects because each component potentially can influence many others through a network of direct and indirect interactions.

Path analysis is one technique that increasingly has been used to quantify causal pathways in networks of interactions. It was originally developed to deal with variables that are correlated because of "a complex of interacting uncontrollable, and often obscure causes" (Wright 1921, p. 557; see also Wright 1934, 1960; Li 1975; Pedhazur 1982). Basically, the technique decomposes the overall correlation between two variables into the direct effects of one on the other, indirect effects mediated by other variables, and spurious effects due to common causes. The computed path coefficients indicate the amount of change expected in the

---

*Author order was determined by a coin toss. Smith is the author to whom correspondence should be addressed; E-mail: fasmith@unm.edu.

†Present address: Department of Biology, California State University, Northridge, California 91330-8303.

dependent variable due to a unit change in the independent variable. Recent applications of path analysis include those in social science (e.g., Pedhazur 1982), evolutionary genetics (Mitchell-Olds 1987; Crespi and Bookstein 1989; Crespi 1990; Arnold and Duvall 1994), physiological ecology (Schemske and Horvitz 1988; Farris and Lechowicz 1990; Mitchell 1994; Smith 1995), and community ecology (Arnold 1972; Wesser and Armbruster 1991; Wootton 1994).

Despite the broad applicability and increasing use of path analysis, there are numerous problems in applying this technique to empirical studies of complex systems. Many authors have noted that path analysis assumes that all important variables are identified; that effects are linear, additive, and unidirectional; and, further, that residuals are not correlated (Wright 1921, 1960; Li 1975; Mitchell 1992, 1993). Some have also recognized that the technique can give different results depending on which components and interactions are included in the path diagram (P. S. Petraitis and A. E. Dunham, unpublished manuscript). Here, we show that even when these conditions are met, path analysis can yield misleading results.

We evaluated path analysis using data from a long-term ecological experiment in the Chihuahuan Desert. Controlled manipulations have demonstrated that kangaroo rats affect other rodents through a network of direct and indirect interactions (Heske et al. 1994). We applied path analysis to data collected from manipulated and unmanipulated systems to assess the ability of the technique to characterize the relationships between kangaroo rats and other rodents.

BACKGROUND AND METHODS

Experiments

In the 1970s, experiments were begun to investigate interactions within communities of desert animals and plants (Brown et al. 1979, 1986). The 20-ha study site is located 6.5 km east and 2 km north of Portal, Cochise County, Arizona. It contains upper-elevation Chihuahuan Desert shrub habitat and is fenced to exclude domestic livestock. Within this area, there are 24 0.25-ha (50 × 50 m) experimental plots. Each is surrounded by a low fence of 6-mm wire mesh that is topped with 15 cm of aluminum flashing (Munger and Brown 1981; Brown and Munger 1985). Access by rodent species to the plots is controlled by different-sized "gates" built into the fences (e.g., Brown and Munger 1985; Heske et al. 1994).

The experimental plots have been subjected to a number of treatments (Brown and Munger 1985; Heske et al. 1994). Six plots, designed to exclude all rodent species, do not have gates and are not considered further. Of the remaining 18 plots, 10 have had kangaroo rats continuously present, four have had kangaroo rats excluded continuously since 1977, and four had kangaroo rats present until 1988, after which they have been removed continuously (fig. 1). Plots with kangaroo rats present had large gates (3.7 × 5.7 cm), which allowed free access by all rodent species. Kangaroo rats were excluded by small gates (1.9 × 1.9 cm), which did not interfere with the movement of the other rodent species (T. J. Valone and J. H. Brown, unpublished manuscript).
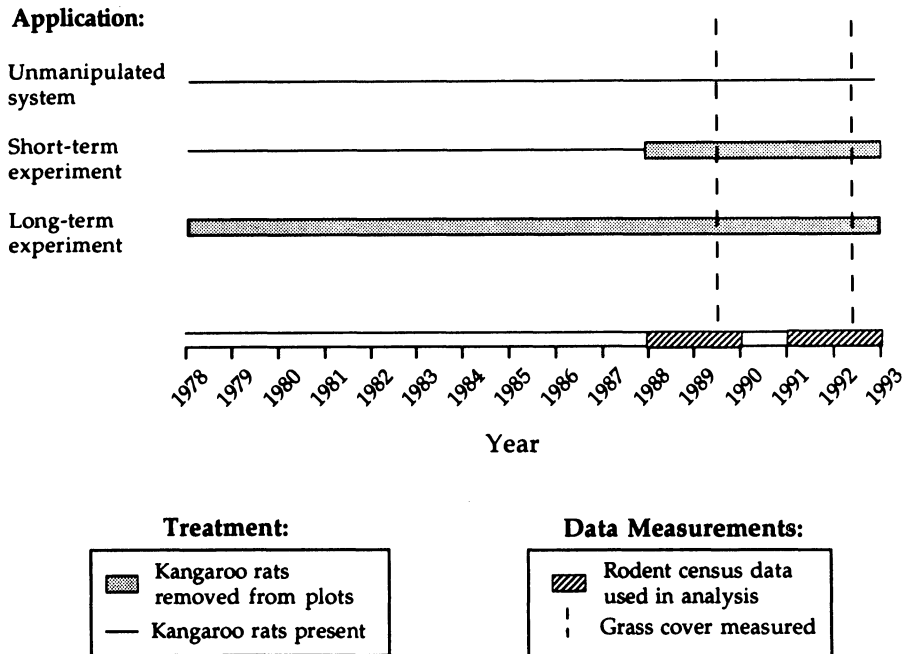
FIG. 1.—Schematic representation of the differences between unmanipulated, short- and long-term kangaroo rat removal plots and the timing of rodent and plant censuses.

Path Diagram and Data

In this community, removal of kangaroo rats (*Dipodomys merriami, Dipodomys ordii,* and *Dipodomys spectabilis*) from experimental plots had three sequential effects. Within the first 2 yr, other common granivorous rodents increased in abundance, apparently in direct response to the absence of their larger competitors (Munger and Brown 1981; Brown and Munger 1985; Heske et al. 1994). Subsequently, after 8–10 yr, grass cover increased dramatically (Brown and Heske 1990a, 1990b; Heske et al. 1993). Finally, the change in vegetation structure led to increased populations of several rodent species characteristic of grassland habitat (Heske et al. 1994). These results suggest that kangaroo rats affect other rodents both directly through competition and indirectly through changes in vegetation, as illustrated in figure 2.

To evaluate these relationships required data on rodent populations and grass cover. Rodents have been censused at approximately monthly intervals since 1977. Within each experimental plot, one live trap was set for one night at each of 49 permanent grid stakes spaced 6.25 m apart. Captured rodents were identified for species, individually marked, weighed, sexed, and released. (For additional details about the experimental design and rodent trapping protocol, see Brown and Munger 1985; Brown and Zeng 1989; Heske et al. 1994.)

Vegetation composition and cover on each plot were measured in early September of both 1989 and 1992 using a point-intercept method. Four transect lines
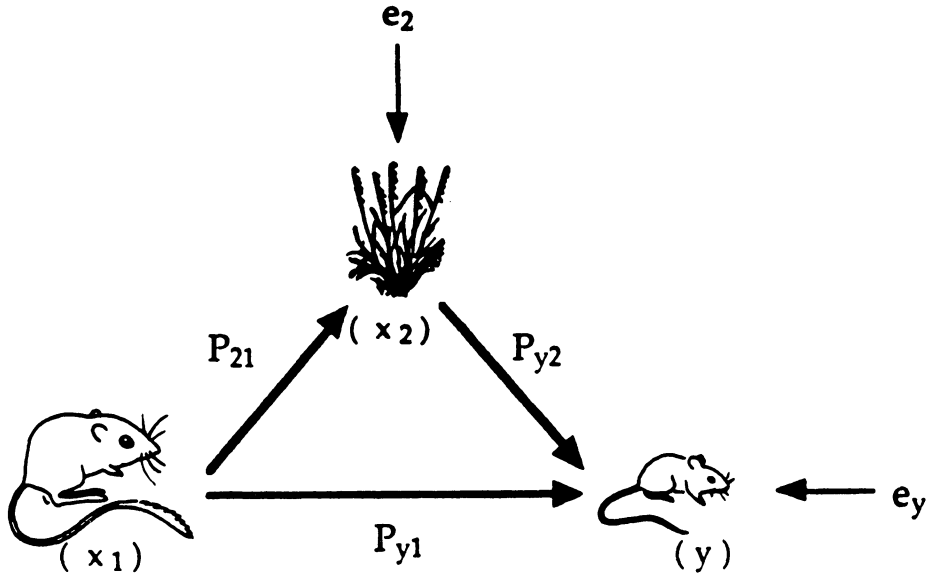
Fig. 2.—Path diagram of hypothesized interactions among kangaroo rats, grass cover, and small granivorous rodents. Here p_{y1} represents the direct negative competitive effect of kangaroo rats on other rodents; p_{21}, the negative effect of kangaroo rats on grass cover; and p_{y2}, the positive effect of grass cover on other rodents. The indirect effect of kangaroo rats on other rodents is the product of the paths p_{21} and p_{y2}. Residual variation is represented by the error terms e_{x2} and e_y and is calculated by $\sqrt{(1 - R^2)}$. This is a fully recursive model; all relationships are presumed to be unidirectional with no feedback loops.

began 8 m from the center of each plot and ran outward toward each corner. All plant species (or bare ground) encountered were counted at 10-cm intervals. For the present analysis of grass cover, we included data for all perennial grass species. (For additional details regarding vegetation sampling and plant responses to kangaroo rat exclusions, see Heske et al. 1994.)

We analyzed the effects of kangaroo rats on two species of small seed-eating rodents, the western harvest mouse (*Reithrodontomys megalotis*) and the desert pocket mouse (*Chaetodipus penicillatus*). These two species were chosen because they were sufficiently abundant to yield reasonable sample sizes and because they were expected to respond differently to the experimental manipulations. Both rodents are primarily granivorous and hence presumably compete directly with kangaroo rats. Harvest mice, however, are most abundant in arid grassland habitats, while desert pocket mice are most abundant in desert shrub habitats (Hoffmeister 1986). Consequently, we expected harvest mice to respond positively to increasing grass cover and pocket mice to respond negatively if at all.

Statistical Analysis

To evaluate the relationships depicted in figure 2, we used path analysis. Like other regression techniques, path analysis assumes that relationships among vari-

ables are linear and additive and that the residuals are not correlated (e.g., Li 1975; Pedhazur 1982). We examined these assumptions for all pairwise combinations of variables and found them to hold reasonably well. In addition, figure 2 assumes that the effects of kangaroo rats on other rodents are unidirectional—that is, recursive without feedback loops. This is an oversimplification, but we have a number of reasons to believe that all three interactions are highly asymmetrical. First, evidence from numerical and energetic compensation and aggressive interference demonstrates that the competitive effects of all small seed-eating rodents on kangaroo rats are negligible (Brown and Munger 1985; Brown and Harney 1993). Second, our experiments show that kangaroo rats strongly inhibit the establishment of grass but that the natural variation of grass cover on our site has no apparent effect on kangaroo rat density (Brown and Heske 1990a; Heske et al. 1993). Third, although grass and vegetative cover influence the abundance and distribution of both harvest and pocket mice (see earlier discussion), there is no evidence for a significant reciprocal effect.

By organizing our data in different but overlapping combinations, we were able to take advantage of the experimental design to conduct a sensitivity test of path analysis. To explore how the technique is influenced by experimental perturbations and natural temporal variation, we assessed its performance in three different applications (fig. 1). Because many previous applications of path analysis have used data from unmanipulated systems, we compared the results of analyses that used only natural variation to those in which additional variation was generated from an experimental perturbation. Further, because direct and indirect interactions can play out with varying time lags, we applied the technique to manipulations of different duration. Thus, we compared three applications.

First, we examined an unmanipulated system. We analyzed only the 10 plots to which both kangaroo rats and all other rodents had free access. This decomposed the overall correlation between kangaroo rats and other rodent species (r_{y1}) into direct and indirect paths based only on the natural level of variation in the system. As such, the application is analogous to the majority of previous uses of path analysis (e.g., Pedhazur 1982; Kingsolver and Schemske 1991; and references therein). This application, however, did not enable us to include the substantial variation created by experimental manipulations.

Second, we analyzed a short-term experiment. To evaluate the ability of path analysis to quantify direct and indirect interactions from the result of a short-term experiment, we used 14 plots: the 10 unmanipulated "control" plots, plus the four from which kangaroo rats had been excluded for less than 5 yr. This design increased the range of variation in the densities of kangaroo rats and other rodents, but the period of kangaroo rat removal was too short to produce substantial variation in grass cover. A possible alternative design—to use just the four short-term removal plots—was rejected because of low statistical power and insufficient variation in the density of kangaroo rats.

Finally, we studied long-term perturbation. To quantify the interactions revealed by a long-term experiment, we used a different combination of 14 plots: the 10 unmanipulated ones, plus the four from which kangaroo rats had been removed for more than 10 yr. This combination of plots produced the widest

range of variation in all variables. Use of just the four long-term removal plots was again rejected because of insufficient power and variation. Similarly, including the four short-term removal plots in this analysis (i.e., using all 18 plots) would have confounded the short- and long-term effects of kangaroo rats on grass cover.

Note that the same 10 unmanipulated plots were used in all analyses. This was necessary to compare the ability of path analysis to detect direct and indirect interactions in unmanipulated versus manipulated systems of varying duration. To avoid pseudoreplication, we used a single value for each variable (grass cover, kangaroo rat density, harvest mice density, and pocket mice density) for each plot so that the sample size was the number of replicate plots subjected to each treatment. For each plot we had many monthly censuses of rodent densities but only two measurements of grass cover, taken in the summers of 1989 and 1992. Consequently, we used rodent densities recorded during the 24-mo period bracketing each plant survey in our analysis (February 1988–January 1990 and February 1991–January 1993).

It is far from straightforward to test for statistical significance in path analysis. Two approaches have usually been taken. The preferable method is to evaluate the entire diagram using maximum-likelihood techniques (e.g., Hayduk 1987; Mitchell 1993; Wootton 1994). Unfortunately, these cannot be applied here because the model (fig. 2) is "just identified"; that is, the number of equations that can be constructed to describe the model is equal to the number of parameters to be estimated. Maximum-likelihood tests can only be applied when the model is "overidentified," that is, when there is more information available than necessary to determine the path coefficients. The other approach generally taken to evaluate path diagrams is to assess the significance of individual paths by calculating the standard errors of the coefficients. Although we have calculated the standard errors of each path coefficient in our model, we urge caution in using these to evaluate the overall significance of direct or indirect pathways. Several authors (e.g., Pedhazur 1982; Kingsolver and Schemske 1991; Mitchell 1993; P. S. Petraitis and A. E. Dunham, unpublished manuscript) have pointed out that such significance testing is of "dubious value," because evaluating the paths independently ignores the correlation structure between the variables, and deleting "nonsignificant" paths may change the correlative structure altogether.

RESULTS

Effects of Experimental Treatments

The basic data are presented in table 1, and they were analyzed using one-way ANOVA. Reflecting the experimental manipulation, densities of kangaroo rats were significantly higher on unmanipulated plots than on both short- and long-term removal plots ($P < .001$). As predicted by figure 1, grass cover was significantly higher on long-term removal plots than on either the unmanipulated or short-term removal plots ($P < .02$). There was also a significant effect of treatment on harvest mouse densities ($P < .001$), which were low on unmanipulated plots and higher on both the short- and long-term kangaroo removal plots. A posteriori

TABLE 1

Summary of Data from Experimental Treatments

| Treatment | N | Kangaroo Rats | | Grass Cover | | Harvest Mice | | Pocket Mice | |
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
A	10	**3.67**	1.24	.102	.049	**.43**	.27	.18	.12
B	4	.16	.10	.088	.012	1.01	.25	.53	.38
C	4	.07	.12	**.256**	.173	1.29	.36	.50	.66

Note.—Treatment A represents the unmanipulated plots; B, the short-term plots; and C, the long-term plots. Values for rodents represent the mean number of individuals per plot per month. Grass cover equals grass present per 1,000 census points. Treatment effects were significant for densities of kangaroo rats, harvest mice, and grass cover (one-way ANOVA, $P < .05$; see the text). Values in bold indicate that means were significantly different from the other treatments in that column (Scheffé procedure, $P < .05$).

contrasts did not detect a significant difference in harvest mice density between the short- and long-term manipulations (Scheffé procedure, $P > .05$). Repeated-measures ANOVA, however, appropriate because we have many measures of harvest mouse numbers on each plot, did find a significant difference between short- and long-term kangaroo rat removal treatments ($P < .05$; Heske et al. 1994). Although pocket mouse densities appeared to be higher on both short- and long-term removal plots than on unmanipulated plots, these differences were not significant in the one-way ANOVA. Again, however, this result is conservative, and repeated-measures ANOVA showed a significant difference between kangaroo rat removal and manipulated plots ($P < .05$; Heske et al. 1994).

Path Analysis: Response of Harvest Mice

Table 2 provides the correlations among variables and the standardized and nonstandardized path coefficients along with their standard errors. Table 3 gives the calculated path equations and residual variation.

When applied to data on harvest mice, path analysis yielded results that differed substantially across the three applications. Analysis of the unmanipulated system revealed a modest overall negative effect of kangaroo rats on harvest mice ($r_{y1} = -0.303$), which was almost entirely due to the direct path ($p_{y1} = -0.230$). The short-term removal experiment yielded a substantially larger overall correlation ($r_{y1} = -0.710$), which again was almost exclusively due to the direct path ($p_{y1} = -0.723$). The long-term experiment also revealed a large overall negative effect of kangaroo rats on harvest mice ($r_{y1} = -0.760$). In this case, however, not only was there a large negative direct effect ($p_{y1} = -0.450$), but there was also a substantial negative indirect effect ($p_{21}p_{y2} = -0.310$). Note not only that the overall correlation between kangaroo rats and harvest mice increased from the unmanipulated system to the manipulated systems but also that the proportion of variance in harvest mice density described by the path diagram increased substantially (table 3). Note also that the path coefficients for the direct effect of kangaroo rats on harvest mice in the short-term application and all three path coefficients in the long-term application were significantly different from zero.

TABLE 2

CORRELATIONS AND PATH COEFFICIENTS

Interaction	r	b	SE	P	β
Harvest mice:					
A Kangaroo rats → harvest mice	− .303	− .050	.071	.505	− .230
Grass → harvest mice	.467	2.361	1.809	.233	.428
Kangaroo rats → grass	− .170	− .007	.014	.638	− .170
B Kangaroo rats → harvest mice	− .710	− .139	.038	**.004**	− .723
Grass → harvest mice	.195	2.102	1.786	.264	.236
Kangaroo rats → grass	.057	.001	.006	.847	.057
C Kangaroo rats → harvest mice	− .760	− .112	.039	**.003**	− .450
Grass → harvest mice	.816	2.399	.656	**.015**	.573
Kangaroo rats → grass	− .542	− .032	.014	**.046**	− .542
Pocket mice:					
A Kangaroo rats → pocket mice	− .212	− .015	.035	.680	− .150
Grass → pocket mice	.390	.926	.886	.331	.364
Kangaroo rats → grass	− .170	− .007	.014	.638	− .170
B Kangaroo rats → pocket mice	− .554	− .077	.034	**.046**	− .561
Grass → pocket mice	.081	.715	1.584	.661	.112
Kangaroo rats → grass	.057	.001	.006	.847	.057
C Kangaroo rats → pocket mice	− .362	.008	.045	.859	.045
Grass → pocket mice	.727	2.336	.765	**.010**	.751
Kangaroo rats → grass	− .542	− .032	.014	.045	− .542

NOTE.—A represents the unmanipulated system; B, the short-term experiment; and C, the long-term perturbation. Also, r represents the correlation between the indicated variables; b, the calculated path coefficient (the partial regression coefficient) and the next column, the associated standard error. Here β represents the standardized path coefficients and was computed from $\beta_{yx} = \mathbf{R}^{-1}r$, where $\mathbf{R}$ is the correlation matrix of independent variables, and r is the column vector containing the correlations between the dependent and independent variables. Path coefficients were tested to determine whether they differed significantly from zero (P); bold type indicates values less than .05.

TABLE 3

CALCULATED PATH EQUATIONS OF THE EFFECT OF KANGAROO
RATS ON OTHER RODENTS

Treatment	Path Equation	e_y
Harvest mice:		
A	− .303 = − .230 − .073	.85
B	− .710 = − .723 + .014	.66
C	− .760 = − .450 − .310	.57
Pocket mice:		
A	− .212 = − .150 − .062	.91
B	− .554 = − .561 + .006	.82
C	− .362 = .045 − .407	.67

NOTE.—A represents the unmanipulated plots; B, the short-term kangaroo rat removals; and C, the long-term kangaroo rat removals. The decomposition of the overall correlation between harvest mice and kangaroo rats is $r_{y1} = p_{y1} + p_{21}p_{y2}$, where p_{y1} represents the direct effect of kangaroo rats on harvest mice, and $p_{21}p_{y2}$ represents the indirect effect via grass cover (see fig. 2). The value e_y represents residual variation due to unknown factors not included in the path diagram and is calculated by $\sqrt{(1 - R^2)}$.

Path Analysis: Response of Pocket Mice

When applied to data for pocket mice, path analysis gave widely varying results across the three applications. Analysis of the unmanipulated system suggested a weak relationship based entirely on the direct path. The short-term manipulation yielded the strongest correlation between kangaroo rats and pocket mice ($r_{y1} = -0.554$), again due entirely to the direct path. The long-term experiment suggested a somewhat lower overall effect of kangaroo rats on pocket mice ($r_{y1} = -0.362$). In this instance, however, path analysis suggested that this was due almost entirely to the indirect effect ($p_{21}p_{y2} = -0.407$). Thus, both the short-and long-term experiments suggested a negative relationship between kangaroo rats and pocket mice, but the short-term attributed virtually all of this to the direct effect, whereas the long-term attributed it to the indirect pathway. As in the case for harvest mice, the proportion of variance explained by the analysis increased with the length of the manipulation. For pocket mice, the only path coefficients significantly different from zero were the direct effect of kangaroo rats in the short-term application and the effect of grass cover in the long-term application.

DISCUSSION

The purpose of this study was to assess the extent to which path analysis can detect direct and indirect interactions in ecological communities. We can first ask whether path analysis can reveal the magnitude of such interactions in the absence of experimental perturbations. The answer is an unqualified no. The strong direct competition between kangaroo rats and the two smaller rodent species demonstrated by earlier studies (Munger and Brown 1981; Brown and Munger 1985; Brown and Heske 1990a, 1990b; Heske et al. 1993; Heske et al. 1994) was detected by path analysis only when data from kangaroo removal plots were included. The wide variation in kangaroo rat density between removal and control treatments was essential to identify the strong effect of direct competition. We attribute the apparent weak direct effect of kangaroo rats on both harvest mice and pocket mice for the nonmanipulated system to habitat selection. Kangaroo rats prefer open areas, harvest mice frequent sites with dense vegetative cover, and pocket mice are associated with shrubs but not grass (Rosenzwieg 1973; Hoffmeister 1986; Bowers et al. 1987).

Given that at least short-term manipulations were necessary to detect the direct interaction, it is not surprising that the only evidence of indirect interactions came from the long-term press experiments (table 3). Path analysis of the long-term data suggested indirect effects of kangaroo rats on both harvest mice and pocket mice. The former result, at least, is consistent with the predictions of figure 2, which was based on earlier analyses (Brown and Heske 1990a; Heske et al. 1994). We conclude that the long-term press experiment was necessary to maintain sufficient variation and to create the temporal sequence of responses necessary to reveal the indirect interaction.

We can now ask whether path analysis applied to the long-term press experi-

ment revealed the full path diagram shown in figure 2. The answer appears to be a rather unsatisfactory "sometimes." In the case of harvest mice, the path equation derived from the long-term data supported the conclusions of earlier studies: that kangaroo rats affect harvest mice directly through competition and indirectly by influencing grass cover. In the case of pocket mice, however, we are at a loss to explain the path equation derived from the long-term data. Information on habitat use by pocket mice would not predict that they should respond positively to increasing grass cover (Rosenzwieg 1973; Hoffmeister 1986; Bowers et al. 1987). The documented competition between kangaroo rats and pocket mice would suggest a strong negative direct effect (e.g., Rosenzweig 1973; Heske et al. 1994), which should have been evident from the long-term and the short-term manipulations.

Results of the path analyses suggested that manipulations were required to reveal direct competitive interactions, and long-term press experiments were required to reveal interactions through indirect pathways with long time lags. These results may not surprise experimental ecologists who have long emphasized the need to manipulate systems to test hypotheses (Bender et al. 1984; Carpenter et al. 1985; Brown et al. 1986; Schmitt 1987; Carpenter 1988; Strauss 1991; Wootton 1992). However, many previous applications of path analysis, especially those in the social sciences, have relied on natural variation (e.g., Pedhazur 1982 and references therein). Even when the technique is applied to experimental data, problems of interpretation remain. Usually only a small subset of the hypothesized pathways are tested directly, because only some of the relevant variables are actually manipulated (e.g., Wesser and Armbruster 1991; Wootton 1994). This problem exists even in using our experimental results to evaluate the simple path diagram shown in figure 2. We manipulated only the densities of kangaroo rats, which permits unambiguous evaluation only of the direct effects of kangaroo rats on other rodents and grass. We did not manipulate grass cover independently of kangaroo rats, although we should have done so to evaluate rigorously the effects of grass on the small rodents.

Not only may experimental perturbations be required to detect interactions, but experiments of different duration may be necessary to reveal pathways with different time lags. A major advantage of a press experiment is that it initiates a sequence of responses that ripple through the system and are resolved on varying timescales. Because the majority of ecological experiments are of short duration compared to the generation times and other response variables of the organisms concerned (Tilman 1989), they may be unable to detect not only indirect interactions but even direct interactions with long time lags. Although the advantage of a long-term press experiment is demonstrated in the difference between our short- and long-term results, these too should be interpreted with caution. Many important interactions may be evidenced only transitorily during a long-term experiment. One example is when indirect effects are opposite in sign and approximately equal in magnitude to direct interactions (e.g., Inouye 1981; Brown et al. 1986). Path analysis does not have any inherent advantage over other techniques in dealing with these problems of interpreting long-term responses.

Interpreting the results of path analysis is further complicated by two related

statistical issues: evaluating the robustness (significance) of a hypothesized path diagram and distinguishing between alternative diagrams. These problems have been discussed by several authors (e.g., Pedhazur 1982; Hayduk 1987; Kingsolver and Schemske 1991; Mitchell 1992, 1993; P. S. Petraitis and A. E. Dunham, unpublished manuscript), and a detailed treatment is beyond the scope of our article. The preferred method of using maximum-likelihood techniques to evaluate the entire model simultaneously could not be applied in the present case (see Background and Methods). The alternative, testing whether the individual path coefficients differ from zero and from each other, has several serious drawbacks (e.g., Pedhazur 1982; Kingsolver and Schemske 1991; Mitchell 1993). We tested whether our path coefficients differed from zero (table 2) but not whether they differed from each other. To do the latter would require an approach such as bootstrapping, which would be hard to justify given our small sample sizes ($N =$ four replicate plots for both the short- and long-term manipulations).

An even less satisfactory way of assessing the "fit" of the model is by determining the proportion of variance that remains unexplained. We report the residual variation (e_y) in table 3. The values for the long-term application are relatively low and fall well within the range reported for most other experimental studies (e.g., Mitchell 1993; Wootton 1994). At least in ecological applications, large residual variations are common and occur even in models that pass maximum-likelihood tests, which suggests an acceptable goodness of fit (e.g., Mitchell 1993; Wootton 1994). Consequently, a large residual error component does not necessarily imply a lack of robustness of the model and may reflect the large role played by environmental variation (Mitchell 1993).

Another concern is the ratio of the number of independent samples to the number of paths being estimated. Ideally, the value should be 10–20 (Mitchell 1993). In reality, few ecological studies attain such ratios (e.g., Arnold 1972; Farris and Lechowicz 1990; Wesser and Armbruster 1991; Wootton 1994), which reflects the effort required to achieve even a minimum acceptable level of replication. Our ratios of sample size to paths range from 3.3 to 4.6. Thus, they are less than the ideal but well above the norm for an ecological study. For example, of 64 path analyses reviewed by P. S. Petraitis and A. E. Dunham (unpublished manuscript), the vast majority had ratios less than 2.

Despite these problems of statistical evaluation, the equations derived from the short- and long-term data for harvest mice do identify direct and indirect interactions that have been demonstrated using other methods (e.g., one-way and repeated-measures ANOVA). Although in some cases the path coefficients and standard errors (table 2) computed for pocket mice are comparable to those obtained for harvest mice, we are reluctant to claim either statistical significance or ecological relevance for these results. We suspect that failure to include one or more critical factors in the model accounts for the uninterpretable results that we obtained for pocket mice (table 2). Not only was our a priori hypothesis about the relationship between grass and pocket mice not supported (in fact, the indirect effect through grass was positive rather than negative; table 3), but we have no explanation for the relationships suggested by the path equations. Although we expect that some critical factor has been left out of the model, neither our experi-

mental results nor the natural history information on pocket mice suggests what
the factor(s) might be.

The need to include all of the critical components and interactions has been
emphasized by numerous authors (e.g., Li 1975; Pedhazur 1982; Mitchell 1992,
1993; references therein). This is particularly a problem in field studies because
the variables and their interactions are almost always embedded in a larger net-
work. Thus, although some of the residual variation is due to experimental and
measurement error, most is due to factors not included in the model. For exam-
ple, three potentially important factors not included in our path diagram (fig. 2)
are the effect of precipitation on grass; the effect of competition among harvest
mice, pocket mice, and other small granivorous rodents; and the effect of preda-
tors on both kangaroo rats and the smaller rodents. We have not included these
factors in our analyses, because only precipitation was measured and none were
manipulated.

We initially applied path analysis to our experimental data because we thought,
based on previous studies, that it offered a potentially powerful way to quantify
the magnitudes of direct and indirect interactions. We have reluctantly come to
conclude that the inferences provided by path analysis were at worst misleading
and at best no better than those already obtained from analyzing the experimental
results with standard statistical techniques (e.g., ANOVA). The problems that
we have encountered in applying path analysis are common to most applications
of the technique in experimental field ecology, in which, because of practical
constraints, the number of replicate samples is low, the unexplained variation
among them is high, and the number of alternative models is potentially large.

CONCLUSION

Scientists in diverse disciplines have been struggling to understand the struc-
ture and dynamics of complex systems. It is difficult to assess the strength and
system-wide consequences of a particular direct or indirect interaction when mul-
tiple components are affecting each other through multiple pathways. Some biolo-
gists have recently followed social scientists in reviving Wright's (1921, 1934,
1960) technique of path analysis. They have applied the technique to complex
networks such as species interacting within ecological communities, different
forces of selection interacting in phenotypic evolution, and different morphoge-
netic processes interacting during ontogenic development (e.g., Arnold 1972;
Roach 1986; Mitchell-Olds 1987; Schemske and Horvitz 1988; Crespi and
Bookstein 1989; Crespi 1990; Farris and Lechowicz 1990; Mitchell 1992, 1993;
Arnold and Duvall 1994; Wootton 1994; Smith 1995). The strength of path analysis
lies in its potential for evaluating specific mechanistic hypotheses. Unlike other
commonly used multivariate techniques, path analysis uses the pattern of correla-
tion among variables to estimate the magnitude of direct and indirect paths. Previ-
ous treatments have emphasized the need to meet certain statistical assumptions
and the importance of including the critical elements in the path diagram (e.g.,
Li 1975; Pedhazur 1982; Mitchell 1994). Our results, however, raise additional
concerns. First, to identify causal pathways, it is necessary to perturb the system.

In the absence of such perturbation, neither path analysis nor any other statistical technique can distinguish causation from correlation. Second, to identify direct and indirect interactions with different time lags, it is necessary to assess the response of the system at different times after the perturbations. Path analysis may be most effective when applied to controlled laboratory experiments or other systems in which it is possible to test the hypothesized causal relationships by manipulating all of the relevant variables and pathways (e.g., Mitchell 1993; Smith 1995).

LITERATURE CITED

Arnold, S. J. 1972. Species densities of predators and their prey. American Naturalist 106:220–236.
Arnold, S. J., and D. Duvall. 1994. Animal mating systems: a synthesis based on selection theory. American Naturalist 143:317–348.
Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65:1–13.
Bowers, M. A., D. B. Thompson, and J. H. Brown. 1987. Spatial organization of a desert rodent community: food additional and species removal. Oecologia (Berlin) 72:77–82.
Brown, J. H., D. W. Davidson, J. C. Munger, and R. S. Inouye. 1986. Experimental community ecology: the desert granivore system. Pages 41–64 in J. Diamond and T. J. Case, eds. Community ecology. Harper & Row, New York.
Brown, J. H., and B. A. Harney. 1993. Population and community ecology of heteromyid rodents in temperate habitats. Pages 618–651 in H. H. Genoways and J. H. Brown, eds. Biology of the Heteromyidae. American Society of Mammalogists, Special Publications, No. 10. Allen, Lawrence, Kans.
Brown, J. H., and E. J. Heske. 1990a. Control of a desert-grassland transition by a keystone rodent guild. Science (Washington, D.C.) 250:1705–1707.
———. 1990b. Temporal changes in a Chihuahuan Desert rodent community. Oikos 59:290–302.
Brown, J. H., and J. C. Munger. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. Ecology 66:1545–1563.
Brown, J. H., and Z. Zeng. 1989. Comparative population ecology of one species of rodent in the Chihuahuan Desert. Ecology 70:1507–1525.
Brown, J. H., O. J. Reichman, and D. W. Davidson. 1979. Granivory in desert ecosystems. Annual Review of Ecology and Systematics 10:201–227.
Carpenter, S. R. 1988. Complex interactions in lake communities. Springer, New York.
Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634–639.
Crespi, B. J. 1990. Measuring the effect of natural selection on phenotypic interaction systems. American Naturalist 135:32–47.

Crespi, B. J., and F. L. Bookstein. 1989. A path-analytic model for the measurement of selection on morphology. Evolution 43:18–28.

Farris, M. A., and M. J. Lechowicz. 1990. Functional interactions among traits that determine reproductive success in a native annual plant. Ecology 71:548–557.

Hayduk, L. A. 1987. Structural equation modeling with LISREL: essentials and advances. Johns Hopkins University Press, Baltimore.

Heske, E. J., J. H. Brown, and Q. Guo. 1993. Effects of kangaroo rat exclusion on vegetation structure and plant diversity in the Chihuahuan Desert. Oecologia (Berlin) 95:520–524.

Heske, E. J., J. H. Brown, and S. Mistry. 1994. Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. Ecology 75:438–445.

Hoffmeister, D. F. 1986. Mammals of Arizona. University of Arizona Press, Tucson.

Inouye, R. S. 1981. Interactions among unrelated species: granivorous rodents, a parasitic fungus, and a shared prey species. Oecologia (Berlin) 49:425–427.

Kingsolver, J. G., and D. W. Schemske. 1991. Path analyses of selection. Trends in Ecology & Evolution 6:276–280.

Li, C. C. 1975. Path analysis: a primer. Boxwood, Pacific Grove, Calif.

Mitchell, R. J. 1992. Testing evolutionary and ecological hypotheses using path analysis and structural equation modeling. Functional Ecology 6:123–129.

———. 1993. Path analysis: pollination. Pages 211–229 in S. M. Scheiner and J. Gurevitch, eds. Design and analysis of ecological experiments. Chapman & Hall, New York.

———. 1994. Effects of floral traits, pollinator visitation, and plant size on Ipomopsis aggregata fruit production. American Naturalist 143:870–889.

Mitchell-Olds, T. 1987. Analysis of local variation in plant size. Ecology 68:82–87.

Munger, J. C., and J. H. Brown. 1981. Competition in desert rodents: an experiment with semipermeable exclosures. Science (Washington, D.C.) 211:510–512.

Pedhazur, E. J. 1982. Multiple regression in behavioral research. Holt, Rinehart & Winston, New York.

Roach, D. A. 1986. Timing of seed production and dispersal in Geranium carolinianum: effects on fitness. Ecology 67:572–576.

Rosenzweig, M. L. 1973. Habitat selection experiments with a pair of coexisting heteromyid rodent species. Ecology 54:111–117.

Schemske, D. W., and C. C. Horvitz. 1988. Plant-animal interactions and fruit production in a Neotropical herb: a path analysis. Ecology 69:1128–1137.

Schmitt, R. J. 1987. Indirect interactions between prey: apparent competition, predator aggregation, and habitat segregation. Ecology 68:1887–1897.

Smith, F. A. 1995. Scaling of digestive efficiency and body size in Neotoma (woodrats). Functional Ecology 9:299–305.

Strauss, S. Y. 1991. Indirect effects in community ecology: their definition, study and importance. Trends in Ecology and Evolutionary Biology 6:206–210.

Tilman, D. 1989. Ecological experimentation: strength and conceptual problems. Pages 136–157 in G. E. Likens, ed. Long-term studies in ecology: approaches and alternatives. Springer, New York.

Wesser, S. D., and W. S. Armbruster. 1991. Species distribution controls across a forest-steppe transition: a causal model and experimental test. Ecological Monographs 61:323–342.

Wootton, J. T. 1992. Indirect effects, prey susceptibility and habitat selection: impacts of birds on limpets and algae. Ecology 73:981–991.

———. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology 75:151–165.

Wright, S. 1921. Correlation and causation. Journal of Agricultural Research 10:557–585.

———. 1934. The method of path coefficients. Annuals of Mathematical Statistics 5:161–215.

———. 1960. Path coefficients and path regressions: alternative or complementary concepts? Biometrics 16:189–202.