

How Good Must Models and Data Be in Ecology?

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SHORT COMMUNICATION

Gary E. Belovsky

How good must models and data be in ecology?

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Abstract Linear programming models of diet selection (LP) have been criticized as being too sensitive to variations in parameter values that have not been or may not be able to be measured with a high degree of precision (small standard error). Therefore, LP's predictions have been questioned, even though the predicted diet choices agree very well with observations in 400 published tests. The philosophical and statistical aspects of this criticism of LP are reviewed in light of the ability to test any non-trivial ecological theory. It is argued that measures of error in field data may not meet simple statistical definitions, and thereby, may make sensitivity analyses that use the error measures overly conservative. Furthermore, the important issue in testing ecological theory may not be the statistical confidence in a single test, but whether or not the theory withstands repeated tests.

Key words Optimal foraging · Linear Programming Philosophy · Sensitivity analysis · Modeling

Introduction

Huggard (1994) is critical of my linear programming model of optimal diet selection (hereafter called LP), because it is too sensitive to variation in input values to take concordance between predicted and observed diets seriously; this is an expansion of an earlier criticism (Hobbs 1990). Both criticisms were developed using a *portion* of the data presented in *one* attempt to validate LP (Belovsky 1986a). The issue of model sensitivity is important, and Huggard's criticisms provide a good context to review statistical and philosophical considerations.

Assessing an ecological model's validity is a problem fraught with difficulties. This issue is not restricted to

model validation, but applies to any hypothesis, because a model is an explicit mathematical statement of a hypothesis. Models hopefully reduce the likelihood of alternative hypotheses producing similar predictions and increase the likelihood of falsification, as compared with qualitative hypotheses. A problem for model validation is posed by model sensitivity (variability predictions, given variation in input parameters).

In more controlled, laboratory sciences, variation in input parameters is equated with measurement error and model sensitivity reflects the potential for error to provide concordance between predictions and observed values (Type I error). However, ecological, especially field, data are notoriously variable, in part due to measurement error, but also due to uncontrollable environmental and individual heterogeneity (e.g., days differ in weather, locations within a habitat differ, individuals differ in size). In addition, an ecological model's input parameters are often computed by combining several different measurements; the variances of computed parameters are not measured but estimated, and this can be problematic (Travis 1982). These modeling, statistical, and philosophical issues are reviewed in the context of Huggard's criticisms of LP.

Modeling issues

Monte Carlo simulation is an appropriate tool for estimating model sensitivity, but the simulation must be correctly constructed and compared with observed data; Huggard's analysis has several flaws. The first flaw is presented by Huggard as a footnote in his Table 2. Two species (*Dissosteira carolina* and *Bison bison*) are excluded from the analysis, because these species' predicted diets did not vary given their standard errors (SEs). Both species are predicted to consume only grass and their observed diets are largely grass, which "anchors" the regression between predicted and observed diets in the region of high grass intake. Therefore, when Huggard discards 2 of 14 comparisons because they are insensitive, he biases his

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analysis to produce an r^2 value lower than reported by me. Would he discard other species as their predicted diets become insensitive with smaller SEs?

The second flaw arises when Huggard assesses sensitivity by varying all LP parameters simultaneously. This is only correct if all the LP parameters for all the species are independent. However, food bulk is the same for all herbivore species in the same environment. Therefore, when Huggard computes an r^2 for one Monte Carlo run of all species, the bulk values must not vary within the run; otherwise, the simulation is equivalent to comparing the species in different environments. Unfortunately, he only does this in some of his simulations.

Finally, Huggard inappropriately compares his results with my study. First, he did not use my raw data, but used rounded values presented by me, and he does not have my observed diets, but estimates them from points on my graph (Belovsky 1986a). This is why he is unable to obtain my reported solution for *Circottetix undulatus* and my reported r^2 . Nonetheless, he evaluates the likelihood of obtaining my results to 3 decimal places.

Statistical issues

Using Monte Carlo simulation, Huggard claims that LP is very sensitive and most sensitive to my standard errors (SE) in cropping rates (i.e., feeding time constraint); this is no surprise, because I stated this in the paper on which he based his critique (Belovsky 1986a: pp. 43–44) and in a subsequent paper (Belovsky 1990a). Moreover, Monte Carlo simulation accurately assesses model sensitivity only if the SEs that it employs accurately represent uncertainty in the model's input parameters. My SEs are *not appropriate* for this analysis, as I stated in Belovsky 1986a (pp. 39–40), because they are *conservative (large) computed estimates*. The SEs are *computed estimates*, because the variance of a parameter is unknown when the parameter is not directly measured, but computed. In addition, the SEs are *conservative*, because the methods used to compute variance employ assumptions that maximize variance, and because the variances of the component measurements used to compute the estimated parameter's variance include environmental and individual heterogeneity as well as error.

Computed SEs

Because cropping rate is the variable driving LP sensitivity, I will use it to exemplify why my reported SE values are inappropriate for Monte Carlo simulation. I computed cropping rates as a product of three values (items/bite X bites/min X g dry mass/item), which were not measured simultaneously (i.e., the number and mass of items removed in a bite could not be associated with a particular set of bites). Therefore, the cropping rates' estimated variances had to be computed using the measured variances for the three component parameters.

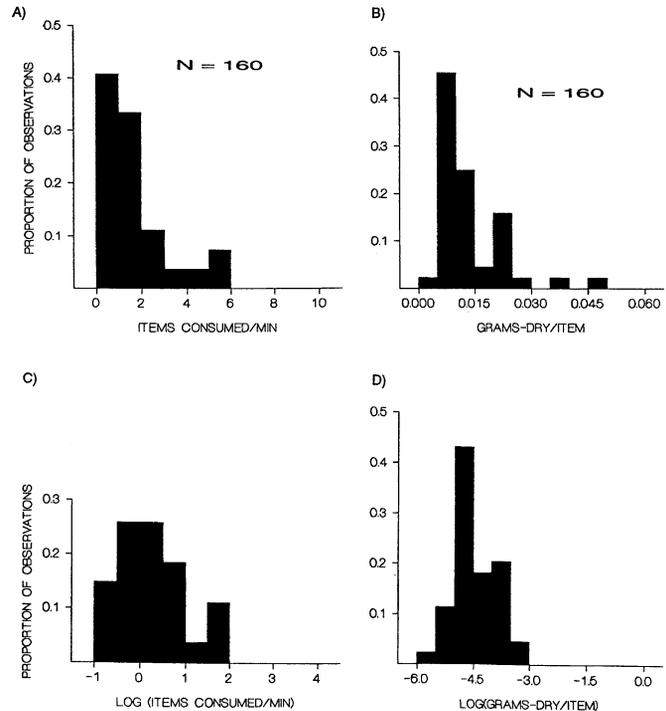


Fig. 1A–D The frequency distributions for the observations of component parameters used to compute the cropping rates of monocots by *Microtus pennsylvanicus* (Belovsky 1986a). This example was chosen because it was typical of all the data employed in computing cropping rates. **A** Data for monocot blades consumed per minute, **B** data for the size of each monocot blade consumed; **C** and **D** present the logarithmic transformations of these data

Cropping rate variances were estimated assuming that component values were normally distributed and independent (Travis 1982); both assumptions are incorrect. First, the components are distributed in a log-normal or negative-exponential fashion (Fig. 1A, B), which would reduce variance estimates. Second, the component parameters are negatively correlated (e.g. Spalinger and Hobbs 1992); I stated this, but did not know the degree of negative correlation so that it could be incorporated into variance calculations (Belovsky 1986a). A negative covariance among components decreases variance estimated for the computed parameter, because the likelihood that all components are large or small at the same time is reduced (Snedecor and Cochran 1967; Travis 1982). Therefore, I opted to conservatively estimate variances by assuming normality and independence and stated this.

Subsequently, I have examined the components of cropping rate to determine their frequency distributions and covariances; this permits an assessment of how conservative my published SEs are. First, the frequency distributions of the components were normalized with a logarithmic transformation (Fig. 1C, D), indicating that 67% of the observations are contained within a range that is 69–78% of ± 1 SD of the untransformed data. Second, simultaneous measures of component parameters

were made with the aid of video equipment, and as expected, they exhibited strong negative covariance (i.e., $r = -0.95$ to -0.98). Finally, using logarithmic transformations of the component's frequency distributions and the observed negative covariances, the re-computed SEs for cropping rates are 40–66% less than those reported by me and used by Huggard.

To illustrate the degree that SE values are reduced and the implications for Huggard's Monte Carlo simulation, I use the SE/mean $\times 100\%$. My original estimates varied between 0.8–41.8% (mean=11.5%), but the more appropriate estimates vary between 0.5–14.8% (mean=4.1%). This means that the range of cropping rate values employed in Huggard's Monte Carlo simulations are on average 2.8 times greater than the 95% confidence interval based on the better estimates of SEs presented here. Therefore, like any model, a Monte Carlo simulation requires appropriate parameters; Huggard did not have these and grossly overestimated LP sensitivity.

Environmental and individual heterogeneity

My reported SEs reflect large amounts of uncontrollable variation as well as measurement error. First, the SE for a species' digestive capacity reflects measurement error, past feeding by the individual, and ontogeny, as organ capacity increases with growth. Second, SEs for plant bulk (wet mass/dry mass) reflect measurement error, differences between and within plant species, and differences between days. Third, SEs for cropping rates reflect measurement error, varying food abundances at different observation locations and differences in body size. Finally, the SE for each species' mean observed diet will reflect measurement error, and differences between individuals based on, for instance, body size, or where they fed. One would like to eliminate or control for all variability, except error, but this is not possible in field ecology. Therefore, what do the SE values really mean?

Using SEs that include environmental and individual heterogeneity, as well as error, Monte Carlo simulation provides an estimate of the SE for each species' predicted diet for comparison with the observed diet's SE. When observed and predicted diets are statistically compared, having SEs for both provides greater power for rejecting hypotheses. This is how Monte Carlo simulations have been employed in other attempts to validate LP (Ritchie 1988; Schmitz 1990). This is not what Huggard attempts with his Monte Carlo simulation.

Observed and "true" mean values in ecology can be very similar, when environmental and individual characteristics are sampled in proportion to their occurrence. However, because this heterogeneity cannot be eliminated, SEs will remain large. Statistically, the only way to reduce SEs is to collect very large sample sizes, which may be prohibitive. For example, using Monte Carlo simulations, I have estimated that sample sizes for cropping rates would have to be as large as 725 in order to reduce my original SEs to a level that meets Huggard's

sensitivity criteria or 260 for the SEs revised here. Even though predicted and observed values can be highly correlated, the Monte Carlo estimated probability of observing this correlation may be minuscule based on SE values inflated by environmental and individual heterogeneity; the latter is what Huggard considers in his critique.

Philosophical issues

If SEs are appropriate, a correctly constructed Monte Carlo simulation *estimates* confidence in a model's predictions, i.e., likelihood of accepting a hypothesis that is false (Type I error). Using Monte Carlo simulation, Huggard concludes that my LP predictions do not warrant confidence and need better validation, but his conclusions may be seriously weakened, given the problems discussed above for SE values and his analysis which overestimate LP sensitivity. Furthermore, Huggard's philosophy and analysis are biased to reject a hypothesis that is true (Type II error). For example, even with his overestimate of sensitivity, his median r^2 values for predicted and observed values fall between 0.73 and 0.93; if these r^2 values do not support LP, will any ecological model and data meet Huggard's standards?

When a bias for Type II error is combined with sampling, statistical and modeling problems that make rejection of a sensitive model likely, a solution for validation is provided by conducting repeated independent tests of the model's predictions. This is akin to asking what is the probability of consistently obtaining a result (number of times observed/total attempts) and consistence suggests that the model providing that result may be valid. Schoener (1983) and Connell (1983) used this approach to test hypotheses dealing with interspecific competition, and most ecologists regularly employ this approach in a less rigorous fashion when comparing results from a variety of studies. This provides a powerful validation tool that minimizes Type I and II error.

The r^2 value in my paper (Belovsky 1986a) on which Huggard bases his critique is a means of summarizing repeated attempts at validation after each predicted diet was shown not to differ statistically from that observed (a point ignored by Huggard). The r^2 value was based upon 14 species in one year, but Huggard ignored an additional 5 comparisons of predicted and observed diets in the same paper. An additional 381 published comparisons of LP predicted and observed diets exist, but Huggard did not allude to them even though he cites some of the papers containing them, including two papers summarizing 73 tests (Belovsky 1986b) and 224 tests (Belovsky and Schmitz 1991). These 400 published tests of LP (Table 1) include studies of mammals, birds and insects, studies of herbivores and omnivores, and studies in boreal forest, deciduous forest, temperate prairie, alpine tundra, arctic tundra, tropical savanna and semiarid shrubland. Given the array of LP tests, why would Huggard call for better and independent validation of LP?

Table 1 A summary of available linear programming diet model (LP) results. The number of cases refers to the number of independent attempts to validate LP predictions. The r^2 refers to the correlation coefficient reported in the study or computed from

the data, where NA refers to an inability to compute the r^2 from the published data. Comments on the studies' general findings are also presented

| Study | Species | No. cases | r^2 | Conclusion |
|-------------------------------------|--|----------------------------------|-------|---|
| Belovsky 1978 | <i>Alces alces</i> | 4 | 0.76 | Energy maximizing or sodium maximizing for females |
| Belovsky 1981 | <i>A. alces</i> | 2 | NA | Energy maximizing |
| Belovsky 1984a | <i>Microtus pennsylvanicus</i> , <i>Tragelaphus strepsiceros</i> | 3 | 0.95 | Energy maximizing |
| Belovsky 1984b | <i>Castor canadensis</i> | 1 | NA | Energy maximizing |
| Belovsky 1984c | <i>Lepus americanus</i> | 2 | NA | Energy maximizing |
| Belovsky 1986a | <i>Dissosteira carolina</i> , <i>Circottetix undulatus</i> , <i>Melanoplus sanguinipes</i> , <i>M. femurrubrum</i> , <i>Microtus pennsylvanicus</i> , <i>Spermophilus columbianus</i> , <i>Sylvilagus nutalli</i> , <i>Marmota flaviventris</i> , <i>Antilocapra americana</i> , <i>Ovis canadensis</i> , <i>Odocoileus virginianus</i> , <i>O. hemionus</i> , <i>Cervus canadensis</i> , <i>Bison bison</i> | 19 | 0.83 | Energy maximizing, except for during the rut are time minimizing |
| Belovsky 1986b | Data on mammalian herbivores from the literature | 28 | 0.86 | Energy maximizing |
| Belovsky 1987a | Human hunter-gatherers (data where parameters are available from specific studies) (data combined from numerous studies) | 5 | 0.99 | Energy maximizing |
| Belovsky 1987b | <i>Microtus pennsylvanicus</i> | 60 | 0.93 | Energy maximizing |
| Belovsky 1987c | <i>Odocoileus virginianus</i> | 6 | 0.76 | Energy maximizing |
| Belovsky and Slade 1987 | <i>Equus caballus</i> , <i>Ovis aries</i> , <i>Bos taurus</i> | 1 | NA | Energy maximizing |
| Belovsky 1990b | <i>Molothrus ater</i> | 4 | 0.98 | Energy maximizing |
| Belovsky 1991 | <i>Rangifer tarandus</i> | 1 | NA | Energy maximizing |
| Belovsky and Slade unpublished work | <i>Circottetix undulatus</i> , <i>Arphia pseudonietana</i> , <i>Melanoplus sanguinipes</i> , <i>M. femurrubrum</i> , <i>Ageneotettix deorum</i> | 8 | 0.96 | Energy maximizing |
| Belovsky and Schmitz in press | <i>Odocoileus hemionus</i> , <i>Ovis canadensis</i> , <i>Cervus elaphus</i> | 23 | 0.84 | Females and immature males are energy maximizing (18 cases), but adult males (5 cases) are time minimizing – including an experimental manipulation of LP |
| Belovsky et al. unpublished work | <i>Oryctolagus cuniculus</i> , <i>Macropus robustus</i> , <i>M. rufus</i> , <i>Ovis aries</i> , <i>Bos taurus</i> | 3 | 0.98 | Energy maximizing |
| Edwards 1993 | <i>Marmota flaviventris</i> | 7 | 0.79 | Energy maximizing except for adult males of one kangaroo species which become time minimizing when mating |
| Doucet and Fryxell 1993 | <i>Castor canadensis</i> | 12 | 0.69 | Energy maximizing |
| Forchhammer and Boomsma in press | <i>Ovibos moschatus</i> | 10 | 0.57 | Energy maximizing – experimental study pairwise comparisons of foods for preferences |
| Karasov 1985 | <i>Ammospermophilus leucurus</i> | 16 (adult females and juveniles) | 0.76 | Energy or sodium maximizing –adult males (5 additional cases) did not appear to be energy or sodium maximizing, or time minimizing; their inclusion reduces r^2 to 0.31 |
| Owen-Smith 1993 | <i>Tragelaphus strepsiceros</i> | 1 | NA | No result because of missing constraint |
| Ritchie 1988 | <i>Spermophilus columbianus</i> | 3 | 0.99 | Energy maximizing, but argued against LP |
| Ritchie and Belovsky 1990 | <i>S. columbianus</i> | 109 field individuals | 0.94 | Energy maximizing |
| Schmitz 1990 | <i>Odocoileus virginianus</i> | 22 captive individuals | 0.81 | Energy maximizing |
| Schmitz et al. 1992 | <i>Lepus americanus</i> | 20 | 0.93 | Energy maximizing |
| Spalinger 1980 | <i>Odocoileus hemionus</i> | 6 | 0.99 | Energy maximizing |
| Vulink and Drost 1991 | <i>Bos taurus</i> | 4 | NA | Energy maximizing – experimental manipulation of LP constraints |
| | | 1 | NA | No result because of missing constraint |
| | | 14 | NA | Energy maximizing |

Does any other ecological model have a comparable array of tests?

The array of LP studies indicates that 99.25% of observed diets are not statistically different from an LP predicted diet (97.5% appear to maximize nutritional intake and 1.75% appear to minimize feeding time, while satisfying nutrient requirements). Only one case (0.25%) is not significantly different from a null model, i.e., foods are ingested in proportion to their availability. Of the 28 studies 20 provide a number of predicted and observed diets so that they can be compared using an r^2 ; the mean r^2 in these studies is 0.87 (SD=0.12). The overall r^2 for all 400 tests is 0.85. This level of concordance is unlikely to arise by chance, and my one r^2 value (0.99) that Huggard criticizes does not appear to be unlikely in the context of the 400 tests.

Conclusion

Contrary to claims by Huggard (1994), Hobbs (1990), Ward (1993), and Owen-Smith (1993, 1994), the high r^2 values obtained in LP studies of diet selection have not made LP a dominant paradigm, creating complacency and stifling research into diet selection and digestive physiology (see Belovsky 1990a). In fact, the LP models have been modified to address additional issues: temporal and spatial diet changes; ontogenetic, sexual and reproductive diet shifts; individual differences in foraging ability; and plant defensive strategies (studies in Table 1 and Ritchie 1988, 1990; Belovsky et al. 1989, 1991; Belovsky and Schmitz 1991). Even nonlinear modifications have been developed and tested (Ball 1994; Belovsky and Schmitz in press). Rather than restricting investigations, LP may foster diversity by providing a conceptual framework that integrates behavioral, physiological and environmental information and consequently, brings together a variety of approaches and data as new insights are incorporated. Furthermore, LP has not been immune to criticism.

There seems to be an underlying philosophical concern expressed by Huggard (1994), Owen-Smith (1993, 1994), Hobbs (1990) and Ward (1992, 1993) in their criticisms. They question the predictive success of a simple model, because the world is complex. LP could be misleading or even wrong, if it is built upon erroneous assumptions (see Hobbs 1990; Belovsky 1990a), but its successes would not indicate this. Therefore, to question LP's successes, one must argue for an inherent flaw in its structure or in data collected to test it.

Owen-Smith (1993) claimed that LP and data used to test it were circular; this was refuted by Belovsky and Schmitz (1993). Huggard (1994) as well as Owen-Smith (1994) have now discarded this concern. Huggard (1994) and Hobbs (1990) raise the issue that parameter estimates are too imprecise (large SE) and this leads to LP predictions that are too sensitive and therefore, unreliable. I question this contention here by illustrating that the SE values are overestimates. The average SE in my

LP studies is 11.5% of its associated parameter: how often are SEs this small in field studies? In addition, numerous independent tests (400) appear to validate LP, regardless of each test's sensitivity. This raises the issue: can any model that *quantitatively* predicts the highly variable responses observed in nature withstand a sensitivity analysis with the SEs typical in ecology?

Critics provide no alternative models with a modicum of LP's predictive power. LP simply indicates how a forager may deal with "trade-offs"; the only other option is the absence of "trade-offs", so that a forager only needs to do well enough to survive and reproduce (satisficing *sensu* Ward 1992, 1993; Owen-Smith 1993). This avoids two issues. First, from a natural selection perspective, doing just well enough may not increase an individual's fitness relative to an individual that assesses trade-offs. Second, from a scientific perspective, satisficing is not testable, since it does not provide predicted values for comparison with observations (Stephens and Krebs 1986; Nonacs and Dill 1993). LP's quantitative predictions make it testable and vulnerable to the issues discussed here. These characteristics of LP and other optimal foraging models make them open to falsification, the essence of a "good" scientific hypothesis.

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