ELSEVIER

Ecological Modelling 162 (2003) 119–143

ECOLOGICAL MODELLING

www.elsevier.com/locate/ecolmodel

Fitting population models from field data

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Received 3 March 2002; received in revised form 8 October 2002; accepted 26 November 2002

Abstract

The application of population and community ecology to solving real-world problems requires population and community dynamics models that reflect the myriad patterns of interaction among organisms and between the biotic and physical environments. Appropriate models are not hard to construct, but the experimental manipulations needed to evaluate their defining coefficients are often both time consuming and costly, and sometimes environmentally destructive, as well. In this paper we present an empirical approach for finding the coefficients of broadly inclusive models without the need for environmental manipulation, demonstrate the approach with both an animal and a plant example, and suggest possible applications.

Software has been developed, and is available from the senior author, with a manual describing both field and analytic procedures.

Published by Elsevier Science B.V.

Keywords: Population models; Prediction; Interaction

1. Introduction

Conservation biology, with its concerns for population viability analysis, risk assessment and the prediction of long-term consequences of management actions, relies increasingly on population and community dynamics modeling. Because of the difficulties in assessing, at least with any accuracy and reliability, the form and intensities of species interactions, these models generally have been built either to deal with only one species at a time or to make greatly simplifying assumptions about the coupled dynamics of non-target species. There also has been a tendency among managers to avoid the difficulties inherent in developing their own, targeted models, and to depend on available software devoted to the application of such simplistic tools as the logistic equation or projection matrices. In many instances, these models have served us well. But researchers and managers should take care in their use, for almost none of them considers both density-dependence and species interactions, and the danger of neglecting either should be obvious: without density-dependent compensation, any change to any demographic parameter in a population currently at or fluctuating about equilibrium must inevitably lead to that population's demise or explosion. It is, therefore, not enough simply to predict that a population will increase or decrease in response to (for example) some

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0304-3800/02/$ – see front matter. Published by Elsevier Science B.V.
doi:10.1016/S0304-3800(02)00390-3

anthropogenic action. With respect to species interactions, it is patently ridiculous to assert knowledge of a population's response to a putative action in the absence of information on that action's impact on the population's food supply, competitors or predators.

There is a growing awareness that much of the interesting dynamics of populations depends critically on the multiple feedback loops inherent in all ecological systems. With respect to managing a deer population, for example, we should know the importance of alternate food sources and how the importance of each food varies with its relative and absolute abundance, the density of the deer population itself and physical aspects of the environment. We also should know how interactions among individuals affect the energy balance of the population, and how food, cover and other physical variables impact such interactions. And we should know the importance of predators, relative to that of various foods or individual interactions, to fitness. And finally, of course, we should know how the deer population feeds back on the food plants and the physical environment that sustain it.

With respect to controlling the invasion of an exotic annual weed like cheat grass (*Bromus tectorum* L.), we should know how soil nutrients affect fitness, not only directly but in synergy, and how important such nutrients are to fitness relative to, say, intra- and inter-specific competition. We should know the effect of grazers, not only with respect to their impact on mortality, but vis-á-vis growth stimulation, and the effects on soil hardness and its consequences for water uptake, and how any growth or mortality stimulating consequences of grazing are secondarily impacted by nutrients, competitors, and physical features of the environment. Finally, as with the deer, we should like to know how the species of interest, in turn, feeds back on soil characteristics, grazers and the physical environment.

In light of the demands for such information the practitioner of conservation biology modeling is faced with a basic problem: How to acquire the necessary information on all the myriad interactions in a timely and cost-effective manner and integrate it into expressions explicitly describing the effects of physical and biotic variables on the target species' biology. Experimentation, bolstered by theory, often can provide good estimates of many of these parameters. But experimental approaches can be time consuming, costly, and sometimes environmentally destructive, often forcing us to rely on questionable estimates of the needed values, sacrifice accuracy, and invite possibly disastrous misjudgments.

An alternative approach is to use field data to fit models empirically. Information obtained from observations can be used to tell us, directly, about the interactions and feedbacks driving a system. Usually, this approach takes the form of regressing local population abundances on environmental variables. It has been used by (for example) Schoener (1974), Crowell and Pimm (1976), Hallett and Pimm (1979), Abramsky et al. (1986) and Morris et al. (2000), with varying rates of success, to estimate the intensity of competition. We support this approach, though with one essential difference. To obtain descriptions of a population's dynamics it is necessary to relate not population densities, but the population growth rate parameter itself, to the underlying environmental variables (see also Morris, 1995). Any such model must take the form:

$$r = f(\{X\}), \tag{1}$$

where r is the per-capita population growth rate, and $\{X\}$ is the set of environmental variables, including densities of conspecifics and other species, affecting it.

2. Methods

Unfortunately, it is rarely possible to evaluate local values of r, a problem that is exacerbated by the likelihood that r may be strongly affected by local microhabitat and by the fact that most animals move about over areas encompassing a variety of such microhabitats. On the other hand, the difficulty of evaluating local r's often can be effectively addressed as follows: Define ρ as the average or, more accurately, the *expected*, per-individual contribution to r of individuals in patches of any one microhabitat, where microhabitat is defined by local environmental characteristics. Inasmuch as the immediate determinants of ρ are survival and reproductive success, ρ is proportional to fitness. We can, therefore, expect natural selection to have endowed creatures with behavioral tendencies that enhance ρ, among which should be the ability to sense and integrate local environmental information, and to respond to what they sense as adverse conditions

by moving to better spots—or, in the case of sessile organisms, to choose the degree of dispersal, to alter their growth or, inasmuch as possible, to exert appropriate control over where they settle. Such behavior will, of course, alter the fitness landscape, thereby promoting continued shuffling of position by all individuals. Inasmuch as these behaviors must be in response to conditions sensed (or recalled) by individuals, the spatial scale of concern may be quite small, encompassing the immediate (or remembered) sensory world of the individual. At this scale any relationships between environment and response are strongest (see also Morris, 1995). If the patches within which each individual senses the quality of its surroundings are small relative to its motility, the time and energetic costs of these movements will be small. Thus, unless movements are socially or physically constrained, individuals should disperse themselves in such manner that ρ tends toward a maximum. But if this is so, individuals should move into patches of the best microhabitats until density feedback drives their fitness contributions down to a common level. We assert, therefore, that ρ should tend toward equality over all occupied microhabitats.

One immediate caveat is critical, however. As Morris (2002) has so effectively pointed out, optimal dispersal does not and cannot lead to equal ρ values at population densities in the range of an Allee effect. Our assertion, therefore, holds only for densities above this range.

The above argument is that advanced for the Ideal Free Distribution (IFD; Fretwell, 1972; Fretwell and Lucas, 1970). Because ρ defines the *expected* per-individual fitness contribution rather than individual contribution, it is considerably more robust. However, in light of the difficulties inherent in the presumption of the IFD, and the importance of our assertion of equal ρ values among microhabitats, we delve into the subject more deeply in Appendix A (see also Abramsky et al., 1991, 1994). For the moment, let us avoid the controversy by presuming we are dealing with a single phenotype (i.e. all individuals are equally effective competitors), in which case the controversy by and large vanishes, and forge on. We urge the skeptical reader to bear with us, for to the degree that the assertion holds, or that deviations can be compensated for, the consequences are of considerable practical importance.

The procedure we suggest is as follows:

1. Construct a population dynamics model, in the form of Eq. (1), for a species of interest (the target species). This should be written in such a manner that a user can build levels of complexity to fit local situations and the availability of data.
2. Randomly sample individuals and, from quadrats centered around each, collect data on the physical environment and on the abundances of foods, conspecifics and other species. The size of these quadrats should correspond to the user's best judgement of a target species' immediate sensory world (but see 'Discussion,' Part 1), and offering easy and energetically minimal (ideally insignificant) access one to another. Violation of the latter consideration may give misleading results, and is a possible explanation for the failure of Abramsky et al. (1986) to find good agreement between regression-based competition estimates and the results of a manipulation study.
3. Make use of the assertion that *expected* individual fitness contributions for any one species tend toward a common value over all occupied microhabitats and that the variance in fitness estimates is, therefore, minimized among individuals. Find the model coefficient values that are consistent with this assertion.

Samples will be characterized by more individuals in regions of higher density. Therefore, to an approximation, the results of this sampling approach can be mimicked by centering quadrats around randomly sampled individuals and counting all individuals of the target species found within these quadrats as sampled individuals in their own right. We do not necessarily encourage this shortcut, but note that it can save considerable time and effort in the field. In this regard, note that we are interested not in a representative description of the environment, per se, but rather in a representative description of how the target species sees it. Thus, if the shortcut sampling scheme is to be followed, the information from each quadrat enters the analysis in proportion to the number of target species individuals it contains—quadrats with, say, 5, 8, 1 and 0 individuals are entered five times, eight times, once and not at all. Mean values, then, relate to means over individuals rather than over quadrats. For those to whom this procedure appears heretical at first,

note that we fall back on the more familiar, randomly distributed quadrat protocol when testing the validity of the coefficients obtained and when applying the fitted model to the task of population and community prediction.

Simple linear models utilizing this rationale have been published previously (Emlen et al., 1989, 1993; Freeman and Emlen, 1995) under the name Interaction Assessment (INTASS).

3. The model

Rosenzweig et al. (1985) found considerable inconsistencies in results based on different approaches to the regression procedure. Much of the problem was attributed to a statistical artifact caused by differences in the variances of the population densities and a correlation between population means and variances. Such an artifact, obviously, would be obliterated were there no variance in the dependent variable and were there no correlation between the dependent variable and population densities. By using ρ as our dependent variable, a quantity that is presumed constant and, therefore, cannot be correlated with mean population density, this artifact is eliminated. Note also, that using contributions to r as our dependent variable makes possible the direct calculation of r. It is simply the mean of those contributions over all individuals.

The forms of species interactions may remain unchanged from one microhabitat to another, their consequences arising strictly from adaptive selection of habitat (D. Morris, personal communication). On the other hand, Abrams (1995) has suggested that as relative environmental conditions, including absolute and relative population densities change, these forms change also. If the latter is true, it serves as a further warning to those who would use simple, linear models. But if a model is sufficiently general, change in form can be approximated in the form of secondary effects. Accordingly, in what follows, we begin with a fairly simple model framework, and then, step-wise, build considerable complexity into it, letting the user decide, based on existing knowledge and the ratio of sample size to number of coefficients required to incorporate the complexity, where to stop. The user should be aware, however, that when there is covariation among variables, the order in which coefficients are solved for can have an impact on their calculated values. This is the other problem encountered in Rosenzweig et al.'s (1985) work. Cognizant of this potential problem, we have built up the model, below, in steps. The reader who wishes to apply the INTASS methodology, may want to built his/her model in a different manner.

The expected contribution of an individual to its population's per-capita rate of change reflects births and growth ultimately slated for reproduction (BRTH), losses from predation, PRED, and non-predative mortality, MORT. Thus,

$$\rho = \mathrm{BRTH} - \mathrm{PRED} - \mathrm{MORT}. \tag{2}$$

The terms BRTH, PRED and MORT are functions of the available foods, which we designate with $\{F_i\}$ (subscripts i), same trophic level species, $\{N_j\}$ with subscripts j (N_T, with subscript $j = \mathrm{T}$, denotes population of the target species), predators and parasites, $\{P_k\}$ with subscripts k, and physical factors, $\{Z_m\}$ with subscripts m. The spatial scale at which the $\{F_i\}$ are defined should reflect the areal extent within which the target species decides whether to accept or reject a food item, in effect the area within which presence of a specific food item can be sensed. This area will be no larger than the quadrats described in point 2, above, and may be considerably smaller. The same scale, as a rule, will hold also for $\{N_j\}$ and $\{Z_m\}$ (though see Section 8). The spatial scale appropriate to $\{P_k\}$ is that within which the *predators* decide whether or not to eat a particular prey item.

The analytic procedure, now, is to treat each individual sampled as a data point, and statistically determine the values of the model's coefficients such that var(ρ) is minimized, i.e. such that the model best fits the assertion of equal ρ values as determined by all individuals' surroundings.

We now propose functions for BRTH, PRED and MORT at increasing levels of completeness and complexity. The user may, as he or she deems fit, stop at any level, or skip any level in the analysis. A summary of all coefficients is given in Table 1.

3.1. Level I: the basic model

All expressions are collapsible to linear functions of the coefficients involved, thereby avoiding the possibility of multiple solutions.

Table 1
Glossary of terms

Fitness terms	
BRTH	Birth rate or, in non-breeding season, contribution of growth ultimately slated for reproduction
PRED	Predation rate
MORT	Mortality by means other than predation. Includes predation by global predators, i.e. those whose presence the target species can avoid only by virtue of habitat choice based on factors other than predator presence, per se
COR	Correction term for source-sink situations, or when lumping sites among which average fitness may differ
Variables	
$\{F_i\}$ (subscripts i)	The set of all nutrient variables (trophic level below the target species) measured at a spatial scale commensurate with the target species' foraging behavior, or both at this scale and at a somewhat larger scale reflecting memory of food locations
$\{N_j\}$ (subscripts j)	The set of all species, including the target species, at the same trophic level as the target species, measured at the same scales as $\{F_i\}$
$\{P_k\}$ (subscripts k)	The set of all predator species, enumerated at a spatial scale commensurate with foraging behavior of the predator in question.
$\{Z_m\}$ (subscripts m)	The set of all physical environmental variables, measured over one or more spatial scales as deemed likely to influence the target species' choice of microhabitat
$\{X_n\}$ (subscripts n)	The set of all global variables, measured over macro-habitats
Coefficients to be found	
$\{v_i\}$	The net value of a food item of type i to growth and reproduction of the target species
$\{\alpha_j\}$	The competitive influence of species j on BRTH
$\{\delta_k\}$	The predation intensity of predator species k on the target species
$\{\xi_m\}$, $\{\kappa_m\}$	The linear and quadratic coefficients describing the effects of physical variable Z_m on MORT
$\{\xi_{B_i}\}$, $\{\gamma_{B_i}\}$	The linear and quadratic coefficients describing the second order importance of food/nutrient i on BRTH
$\{\xi_{B_j}\}$, $\{\gamma_{B_j}\}$	The linear and quadratic coefficients describing the importance of secondary, same-trophic-level species j on BRTH
$\{\xi_{B_k}\}$, $\{\gamma_{B_k}\}$	The linear and quadratic coefficients describing the importance of predator k to BRTH
$\{\xi_{B_m}\}$, $\{\gamma_{B_m}\}$	The linear and quadratic coefficients describing the importance of physical environmental factor m on BRTH
$\{\xi_{P_i}\}$, $\{\gamma_{P_i}\}$	The linear and quadratic coefficients describing the importance of food/nutrient i on PRED
$\{\xi_{P_j}\}$, $\{\gamma_{P_j}\}$	The linear and quadratic coefficients describing the importance of same trophic level species j on PRED
$\{\xi_{P_k}\}$, $\{\gamma_{P_k}\}$	The linear and quadratic coefficients describing secondary effects of predator k on PRED
$\{\xi_{P_m}\}$, $\{\gamma_{P_m}\}$	The linear and quadratic coefficients describing the impact of physical environmental variable m on PRED
$\{\xi_{\mathrm{MB}}\}$, $\{\gamma_{\mathrm{MB}}\}$	The linear and quadratic coefficient describing the importance of BRTH-determining factors on MORT (e.g. starvation)
$\{\xi_{\mathrm{MP}}\}$, $\{\gamma_{\mathrm{MP}}\}$	The linear and quadratic coefficients describing the secondary importance of predators on MORT
$\{\xi_{\mathrm{MN}}\}$, $\{\gamma_{\mathrm{MN}}\}$	The linear and quadratic coefficients describing the secondary importance of same-trophic-level species on MORT
$\{\theta_n\}$	The coefficients describing the effect of macro-habitat variable n on fitness of the target species
$\{\tau_i\}$	The handling time for an individual of the target species on a food item of type i
$\{\tau'_j\}$	The handling time for a predator on an item of prey species j

Let $0 < \alpha_{ij} \ll 1$ be the probability that a consumer of the target species, $j = \mathrm{T}$, captures and utilizes an encountered item of food i in some very small unit of time and in the absence of competition. Then the probability it acquires and uses the item when conspecific competitors are about is

$$\alpha_{i\mathrm{T}}(1-\alpha_{i\mathrm{T}})^{N_j-1} = \left(\frac{\alpha_{i\mathrm{T}}}{1-\alpha_{i\mathrm{T}}}\right)(1-\alpha_{i\mathrm{T}})^{N_j}.$$

In the presence of competitors of other species, $\{j\}$, this probability becomes

$$\left(\frac{\alpha_{i\mathrm{T}}}{1-\alpha_{i\mathrm{T}}}\right)\prod_j (1-\alpha_{ij})^{N_j}$$

so that the total amount eaten is

$$\sum_i F_i \left(\frac{\alpha_{i\mathrm{T}}}{1-\alpha_{i\mathrm{T}}}\right)\prod_j (1-\alpha_{ij})^{N_j}.$$

If we presume that the reproductive rate (or, in the non-reproductive season, the rate at which growth

ultimately slated toward reproduction occurs), is proportional to the rate at which nutritional value is taken in, and let v_i be the nutritional value of an item of type i, then we can write a first estimate of BRTH as

$$\mathrm{BRTH} = \sum_i v_i F_i \left(\frac{\alpha_{i\mathrm{T}}}{1-\alpha_{i\mathrm{T}}} \right) \prod_j (1-\alpha_{ij})^{N_j}.$$

The contribution to births must, however, incorporate metabolic costs unrelated to acquisition and the possible use of existing reserves. We combine these into a constant, β, and write

$$\mathrm{BRTH} = \beta + \sum_i v_i F_i \left(\frac{\alpha_{i\mathrm{T}}}{1-\alpha_{i\mathrm{T}}} \right) \prod_j (1-\alpha_{ij})^{N_j}.$$

We now make use of the very small magnitudes of the alphas and approximate the above with

$$\begin{aligned}\mathrm{BRTH} &= \beta + \sum_i \alpha_{i\mathrm{T}} v_i F_i \left(1 - \sum_j \alpha_{ij} N_j \right) \\ &= \beta + \sum_i \alpha_{i\mathrm{T}} v_i F_i - \sum_j \left(\sum_i \alpha_{i\mathrm{T}} v_i \alpha_{ij} F_i \right) N_j.\end{aligned}$$

This leaves us with the problem, with several foods and several same-trophic level species, that the number of coefficients to be fit may become very large. To avoid this problem, we further simplify, approximating $\sum_i \alpha_{i\mathrm{T}} v_i \alpha_{ij} F_i$ by α'_j. Our expression now becomes

$$\mathrm{BRTH}^{(1)} = \beta + \sum_i v'_i F_i - \sum_j \alpha'_j N_j : v'_i \equiv \alpha_{i\mathrm{T}} v_i. \tag{3}$$

For future reference, we abbreviate $v'_i F_i$ with B_i, $\alpha'_j N_j$ with A_i, so that

$$\mathrm{BRTH}^{(1)} = \beta + \sum_i B_i - \sum_j A_j.$$

This coalescing of terms unfortunately leads to a less precise definition of the coefficients. However, $\{v'\}$ still indicates value, weighted by acceptability (which, after all, should reflect value), and $\{\alpha'\}$ corresponds to the more familiar species interaction terms of the Lotka–Volterra equations. The superscript on BRTH denotes that this is the first, or level I analysis.

Note, before moving on, that the F-values need not be simply food abundances; they could be calculated, food-related values based on some model. For example, Beauchamp et al. (1999) note that encounter rates of fish with various prey types can be written as (roughly) proportional to search volume times prey density, where search volume is proportional to reaction distance squared times swimming speed, and reaction distance varies with the square root of light level times length of a prey item. Such calculated encounter rates might be used to advantage in place of abundances, per se.

Predation, in its simplest form, will vary with the numbers of predators and the intensity of predation by each. Therefore,

$$\mathrm{PRED}^{(1)} = \sum_k \delta_k P_k, \tag{4}$$

where δ_k is the intensity of the predation by predator k.

The level of mortality from non-predatory causes must be highly dependent on the physical environment. However, it is unlikely that we can depend on MORT consistently rising or falling with the value of any particular value; there often will be an intermediate value at which MORT is maximum, or minimum. Thus, as a first approximation, it is convenient to write

$$\mathrm{MORT}^{(1)} = \mu + \sum_m \xi_m Z_m + \sum_m \kappa_m Z_m^2, \tag{5}$$

where μ is non-predative mortality under ideal environmental conditions.

The procedure, now, is to use a computer algorithm to find the values of $\{v'_i\}$, $\{\alpha'_j\}$, $\{\delta_k\}$, $\{\xi_m\}$, and $\{\kappa_m\}$ that minimize var(ρ). Because this procedure depends on the existence of density feedback, α'_{T} must be scaled to some positive value (say 0.01 or 0.001). The resulting ρ, therefore, is proportional, rather than equal to true fitness.

Before proceeding, note that $\{v'\}$ is more than simply net nutritional value; the impact of a food on reproduction is, for example, enhanced by any synergy between it and other foods and if the presence of a food interferes with access to a better food, its value is diminished and may even become negative. These secondary effects could, in theory, be dealt with in a later analytic step, but accuracy is enhanced if they can be incorporated up front. In the same vein, though it rather spoils the rigor of the derivation above, the

alpha values can reflect not only competition, but (say) cooperative feeding. Therefore, realistically, they, too, can become negative. Predation, also, can take negative values if thinning of the herd results in the emergence of healthier individuals (or, in the case of plants, if thinning of foliage enhances survival or stimulates production). Finally, because this leaves no constraints on the coefficients, the analysis (level I only) is equivalent to a multiple regression with N_T (the subscript T denoting the target species) as the dependent variable.

3.2. Higher level analyses

Several modifications of the basic model follow. The user may opt to apply any, all, or none, so long as they are entered into the analysis independently (see Section 4). Note that the order in which these modifications are entered into the analysis may affect the results, or lead to cases where the number of coefficients to be solved exceeds a reasonable number in light of sample size. The user, therefore, is advised to proceed with caution. Based on analyses of several data sets, as well as standard statistical rules of thumb, the number of quadrats should be at least 5, and ideally more than 10 times the number of variables.

3.2.1. Secondary impacts of {F}, {N}, {P} and {Z}

Physical factors clearly can impact both BRTH and PRED. In addition, BRTH may be enhanced by cooperative hunting, or negatively impacted by harassment (e.g. see Brown et al., 1988); predation may be exacerbated by a tendency for large numbers of prey to attract predators or be ameliorated by group defense behavior. An abundance of predators may intimidate foragers into spending less time in search of food (see Brown et al., 1988), or force them into habitat where they are more exposed to non-predative mortality; predators of one species may influence other predators to shift food preferences. And grazing may stimulate plant growth. Thus, higher trophic levels also can exert influences on BRTH and PRED. Finally, the values of various foods may be affected by synergistic, physiological interactions, and the abundance of any one may alter search image patterns. Because they may vary nonlinearly, a convenient (and easily interpretable) form of expression for these effects is (e.g. for the effect of nutrients on BRTH)

$$\exp\left\{\sum_i \xi_{B_i} F_i + \sum_i \gamma_i F_i^2\right\}.$$

In fact, if we presume an already good fit, computation can be enormously simplified if the above is approximated by

$$1 + \sum_i \xi_{B_i} F_i + \sum_i \gamma_i F_i^2.$$

Over all modifying terms, therefore, we have

$$\begin{aligned}\mathrm{BRTH}^{(n)} = \beta + (\mathrm{BRTH}^{(n-1)} - \beta) \\ \times \left\{\left[1 + \sum_i \xi_{B_i} F_i + \sum_i \gamma_{B_i} F_i^2\right]\right. \\ \times \left[1 + \sum_i \xi_{B_j} N_j + \sum_j \gamma_{B_j} N_j^2\right] \\ \times \left[1 + \sum_i \xi_{B_k} P_k + \sum_{ik} \gamma_{B_k} P_k^2\right] \\ \times \left.\left[1 + \sum_i \xi_{B_m} Z_m + \sum_m \gamma_{B_m} Z_m^2\right]\right\},\end{aligned} \tag{6}$$

where the superscripts, n and $n-1$ refer to the level of analysis. Similarly,

$$\begin{aligned}\mathrm{PRED}^{(n)} = \mathrm{PRED}^{(n-1)} \left\{\left[1 + \sum_i \xi_{P_i} F_i + \sum_i \gamma_{P_i} F_i^2\right]\right. \\ \times \left[1 + \sum_i \xi_{P_j} N_j + \sum_j \gamma_{P_j} N_j^2\right] \\ \times \left[1 + \sum_i \xi_{P_k} P_k + \sum_{ik} \gamma_{P_k} P_k^2\right] \\ \times \left.\left[1 + \sum_i \xi_{P_m} Z_m + \sum_m \gamma_{P_m} Z_m^2\right]\right\}.\end{aligned} \tag{7}$$

Occasionally, there may be a very high correlation between a variable used in one of the above expressions and its square. In such cases it is not appropriate to use the squared term, and the corresponding gamma values should be set to 0.

3.2.2. Impacts of BRTH and PRED on MORT

Non-predative mortality can be impacted by the effects of food, competition or predation on dispersion and, thus, exposure to the physical environment. Accordingly, we write

$$\begin{aligned}\mathrm{MORT}^{(n)} &= \mu + (\mathrm{MORT}^{(n-1)} - \mu) \\ &\times \Bigg\{ [1 + \xi_{\mathrm{MB}}\mathrm{BRTH}^{(n-1)} + \gamma_{\mathrm{MB}}(\mathrm{BRTH}^{(n-1)})^2] \\ &\times \left[1 + \sum_j \xi_{\mathrm{M}N_j} N_j + \sum_j \gamma_{\mathrm{M}N_j} N_j^2 \right] \\ &\times [1 + \xi_{\mathrm{MP}}\mathrm{PRED}^{(n-1)} + \gamma_{\mathrm{MP}}(\mathrm{PRED}^{(n-1)})^2] \Bigg\}. \end{aligned} \tag{8}$$

3.2.3. Functional response for target species

BRTH, as formulated above, is based on the presumption that the act of acquiring and consuming food takes no time. If we let $0 < \tau_i'' \ll 1$ be the handling time per item of food i, relative to some standard time unit, such as a day, then the time used in food handling is

$$\sum_i (\text{Number of items type } i \text{ eaten})\, \tau_i''.$$

The value of β is not affected by time spent feeding. Therefore, to account for the loss in time available for finding new food items, we suppose that G_i, the amount of food i eaten in the standard time unit under the presumption that $\tau_i \ll 1$, $\forall$: i, is proportional to F_i, with a proportionality coefficient a_i. Then

$$\begin{aligned} G_i &= a_i F_i \left[1 - \sum_i \tau_i'' G_i \right] \\ &= a_i F_i \left[1 - \sum_i a_i \tau_i'' F_i \left(1 - \sum_i \tau_i'' G_i \right) \right] \\ &= \cdots = a_i F_i \left[1 - \left(\sum_i a_i \tau_i'' F_i \right) + \left(\sum_i a_i \tau_i'' F_i \right)^2 \right. \\ &\quad \left. - \left(\sum_i a_i \tau_i'' F_i \right)^3 \right] + \cdots = \frac{a_i F_i}{1 + \sum_i a_i \tau_i'' F_i} \\ &= \frac{a_i F_i}{1 + \sum_i a \tau_i F_i} : \tau_i = a_i \tau_i'', \end{aligned}$$

so that

$$\mathrm{BRTH}^{(n)} = \frac{\sum_i B_i^{(n-1)}}{1 + \sum_i \tau_i F_i} - \sum_j A_j^{(n-1)}.$$

For ease of computation (it permits us to use a regression), this expression is approximated with

$$\mathrm{BRTH}^{(n)} = \sum_i B_i^{(n-1)} \left(1 - \sum_i \tau_i F_i \right) - \sum_j A_j^{(n-1)}. \tag{9}$$

3.2.4. Functional response for predators

Let G_j be the amount of food j taken in by an individual of predator species k where handling time, τ_{jk}'', is insignificant. Then

$$\begin{aligned} G_j &= \delta_k N_j \left(1 - \sum_j \tau_{jk}'' G_j \right) \\ &= \cdots = \delta_k N_j \left(1 - \delta_k \sum_j \tau_{jk}'' N_j \right) \\ &\approx \frac{\delta_k N_j}{1 + \sum_j \tau_j' N_j} : \tau_j' = \delta_k \tau_{jk}'' \end{aligned}$$

so that

$$\mathrm{PRED}^{(n)} = \frac{\mathrm{PRED}^{(n-1)}}{1 + \sum_j \tau_j' N_j}.$$

Again, for ease of computation, we approximate this with

$$\mathrm{PRED}^{(n)} = \mathrm{PRED}^{(n-1)} \left(1 - \sum_j \tau_j' N_j \right). \tag{10}$$

4. Computation and statistics

4.1. Level I

Because shuffling of individuals among microhabitat patches is the mechanism by which the proposed distributions occur, and because the critical element

affected is local number of individuals, we move the N_T term in Eq. (3) to the left side of the equation and use it as the dependent variable in a multiple regression. The appropriate estimates of the various coefficients, $\{v'\}$, $\{\alpha'\}$, $\{\delta\}$, $\{\xi\}$ and $\{\kappa\}$, are given accordingly. The user may scale α_T, the conspecific density feedback on BRTH, to (say) 0.1 or 0.01, in which case all other coefficients obtained from the regression must be corrected also by a factor of 0.1 or 0.01.

4.2. Level II

To find the coefficients corresponding to later steps in the analysis, note (e.g. for the effects of food on BRTH) that

$$\begin{aligned}\rho^{(n)} &= \text{constant} + \varepsilon \\ &= \text{BRTH}^{(n-1)}\left[1 + \sum_i \xi_{B_i} F_i + \sum_i \gamma_{B_i} F_i^2\right] \\ &\quad - \text{PRED}^{(n-1)} - \text{MORT}^{(n-1)} \\ &= \rho^{(n-1)} + \sum_i \xi_{B_i} \text{BRTH}^{(n-1)} F_i \\ &\quad + \sum_i \gamma_{B_i} \text{BRTH}^{(n-1)} F_i^2.\end{aligned}$$

Thus,

$$\begin{aligned}\rho^{(n-1)} &= -\sum_i \xi_{B_i} \text{BRTH}^{(n-1)} F_i \\ &\quad - \sum_i \gamma_{B_i} \text{BRTH}^{(n-1)} F_i^2 + \text{constant} + \varepsilon.\end{aligned}$$

and the values of $\{\xi_{B_i}\}$ and $\{\gamma_{B_i}\}$ can, again, be found by regression using the just previously calculated $\rho^{(n-1)}$ as the dependent variable.

Statistically, the step-wise mode of solution must be undertaken with care because the apparently easy, continual buildup of fitted coefficient values may outrun sample size. By using a bootstrap procedure (Scheiner and Gurevitch, 1993) over all quadrats, on all analytic steps taken together, the calculated error variance should be quite reliable. However, we caution the user to act conservatively, subtracting degrees of freedom as indicated by the standard BonFerroni procedure. Note, though, that any higher level of analysis has no effect on the results or statistics of prior level analyses.

5. Tests of biological validity

Because of the controversy surrounding our (modified IFD) presumption of equal fitness values among occupied microhabitats (see Appendix A for references), tests of the accuracy with which the model fits real life situations is mandatory. Suppose fitness (ρ) expressions are determined for K species in a community, and that the bulk of information necessary to describe these fitnesses is contained in the data collected. Four tests of the predictive validity of INTASS are then possible.

1. After finding the model coefficients for each of these species, using data from quadrats centered about randomly sampled *individuals*, apply the resulting models to an independent data set from randomly distributed *quadrats* to predict, quadrat-by-quadrat, the local densities of these K species (i.e. for each quadrat, the density most closely providing the hypothetical, fixed value of ρ). Compare the predicted values with those observed.
2. Alter the environment in some specified manner—remove a predator or alter the relative or absolute abundances of food, for example, and use the derived expressions to simulate the response and ultimate, new equilibrium configuration of species. A true equilibrium may never, in fact, come about or even have existed initially, but the predicted equilibrium should approximate the observed central tendencies.
3. Laboratory and/or field experiments can be used to determine secondary effects (such as, e.g. the importance of pH to uptake of some soil nutrient). Do the patterns and intensities of such second order effects, as found from laboratory or field work, follow the form suggested by the INTASS-derived gamma and csi values?
4. Ongoing or completed studies provide us with considerable information on (for example) food preferences, predator avoidance, the role of physical environmental factors on population dynamics. Does the information provided by an INTASS

analysis jibe with these previously determined relations?

6. The case for plants

Note that variance in fitness is to be minimized over *individuals*. The concept of individual is clear in the case of animals, less so for plants. In addition, whereas animals can move about freely, thereby making the assertion of equal expected fitnesses at least a reasonable possibility, plants are sessile. But if this approach cannot be applied to the most basic units of a community, it certainly will not prove terribly useful. Can it work for plants?

When one defines "individual" as the seed, the assertion of equal fitnesses applies at least to annual plants, for seed production, like movement in animals, constitutes an expansion into appropriate microhabitats. When fitness, defined as the number of seeds produced per seed, is high, more seeds, and potentially more biomass, accumulates, all else being equal, leading to suppression of fitness by density feedback. The enormous plasticity in plants allows density feedback to occur via growth, form, flowering, pollination, seed production, seed abortion and seed dormancy (Kay and Harper, 1974; Harper, 1977), as well as dispersion. Such responses permit rapid fitness responses to local conditions so that, as with animals, fitness can be expected to converge rapidly across quadrats toward a constant value characteristic of the global conditions of the site as a whole. And rapidity, of course, is vital to a valid application of INTASS. In this regard, there is considerable experimentation indicating that huge inequities (up to 4 orders of magnitude) in the densities of seeds sown, in monospecific plots, invariably lead to near equality (a factor of 2, 3 or less in most cases and never more than 7) in the density of seeds produced by those sown plants in their *first* reproductive season (Harper and Gajic, 1961; Palmblad, 1968; Harper, 1977). A proportional reduction in ratio over a second season would lead to effectively equal fitnesses. Experiments by Freeman using mixed plots of *Bromus rubens* and *Lepidium densiflorum*, with seeds sown at (total) densities of 1/10, 1/50, and 1/100 cm^2, and ratios of 1:2, 1:1, and 2:1, indicated a return to equal fitnesses across plots within two generations, *even when possible density feedback inherent in early survival was negated by replacing dead plants* (Freeman and Emlen, in preparation).

To define fitness in perennials, we must look at a weighted sum of contributions from both seed and vegetative reproduction, that is, something akin to net primary production (NPP). How should the two be weighted? Many plants produce seeds only once in a few, benign years. Others, such as pines, produce an enormous bumper crop in response to extreme stress. Seed production, therefore, cannot be considered a reliable measure of fitness except, perhaps, when averaged over long time periods. Also, growth, as an indicator of good environmental conditions, may serve as a crude estimator of seed production, on average. Taken together this reasoning points to units of NPP as the most reliable and consistent (year-to-year) measure of "individuals." As such, fitness contribution in a given year becomes the (log) ratio of NPP in that year to the year previous. On the other hand, plants can persist and grow for a long time while remaining sterile. Thus, it may be advisable to repeat INTASS analyses using both NPP and seeds as units of individuals.

A final consideration: both seed production and NPP reflect not only environmental conditions, but the size of the "pool" that gives rise to them; a large perennial will produce more seeds and more NPP than a small one, all else being equal. We, therefore, need to correct our "individual" count for parent plant size. To do this, we suggest measuring cover of both the "parent" plant, (X_P) that about which the quadrat is centered and from which seed and/or NPP data are collected, and total cover (X_T) of the target species in each quadrat. Then, using a simple but very general model,

$$\text{NPP or number of seeds} = aX_P^{\alpha} \exp\{\beta X_P\},$$

a (log–log) regression over all quadrats will generate a general production–plant size relationship. This may be used to scale production to plant size, yielding a measure of "Corrected" number of "individuals" = (NPP or number of seeds)/($aX_P^{\alpha} \exp\{\beta X_P\}$). Note that this procedure applies only to perennials.

Two changes in the model are required when dealing with plants as target species. First, there is no term equivalent to handling time. Thus, τ values are set automatically to 0. Second, whereas foods for animals are viewed as complimentary, plants require certain essential nutrients for survival and reproduction (Salisbury and Ross, 1992, see 'Discussion' in

Chapter 2; Tilman, 1982). That is, no growth can occur in the absence of any critical nutrient. Accordingly, instead of writing nutrient value taken in as a weighted sum, we need to view it as the logarithm of a weighted product. Thus, we write

$$\mathrm{BRTH}^* = \sum v_i' \ln\left[F_i \prod_j (1-\alpha_j)^{N_j}\right].$$

However, as written, the results will differ depending on the measurement scale used for $\{F\}$. Thus, we need to incorporate a scaling factor. This was not necessary in the case of animals because the scaling factor could be subsumed in $\{v\}$. We write

$$\begin{aligned}
\mathrm{BRTH}^* &= \sum_i v_i' \ln\left[c_i F_i \prod_j (1-\alpha_j)^{N_j}\right] \\
&= \sum_i c_i v_i' + \sum_i v_i' \ln\left[F_i \prod_j (1-\alpha_j)^{N_j}\right] \\
&= \sum_i c_i v_i' + \sum_i v_i' \ln(F_i) \\
&\quad + \sum_i v_i' \ln \prod_j (1-\alpha_j)^{N_j} \\
&= \sum_i c_i v_i' + \sum_i v_i' \ln(F_i) + \sum_i v_i' \ln(1-\alpha_j)^{N_j} \\
&\approx \sum_i c_i v_i' + \sum_i v_i' \ln(F_i) - \sum_i v_i' \sum_j \alpha_j N_j \\
&= \beta + \sum_i v_i' \ln(F_i) - \sum_j \alpha_j' N_j : \beta \\
&\equiv \sum_i c_i v_i', \alpha_j' \equiv \left(\sum_i v_i'\right) \alpha_j. \qquad (11)
\end{aligned}$$

The expression, therefore, is exactly that used for animals, except that $\{\ln(F_i)\}$ is used in place of $\{F_i\}$.

7. Examples of applications

7.1. Animals

We applied the above model to data collected by Kirchhoff (1994) on an island-hopping population of southeast Alaskan black tailed deer, *Odocoileus hemionus*. Despite the fact that the islands vary in size, each constitutes a semi-isolated site within which the deer presumably gather information on resources, predation risk, physical and social conditions, and decide whether to stay or move on to another island. Accordingly, we considered each of the 97 islands a quadrat. A year long, time-integrated measure of deer density on each island was estimated from number of pellet clusters observed in the spring (recall that it is relative rather than absolute local abundance that applies in the analysis; number of pellet clusters provides an estimate of relative occupation). Potential resources include red huckleberry, *Vaccinium parvifolium*; blueberry, *V. ovalifolium* and *V. alaskensis*, other shrubs (*Gaultheria shallon*, *Menzesia ferruginea* and herb layer *Vaccinium*) and deciduous forbs (lumped in this analysis according to whether they hold their leaves over winter (winter forbs) or not (summer forbs)). Of the shrubs, only huckleberry and blueberry occurred on more than 6 of the 97 islands and, accordingly, in the interests of minimizing number of coefficients to be found, all others were dropped from the analysis. Units of potential food abundance were in kg available biomass per ha. Predation comes from occasional wolf (*Canus lupus*) forays originating from one very large (Prince-of-Wales) island. The wolves appear to drive deer to the more distant islands where their otherwise unexplainably high densities significantly lower the food supply. Measured physical variables included island size, effective island size (cumulative island area, in hectares, of all wolf-free islands within 500 m of the sample island reachable by swims of 250 m or less), swimming distance (km) from the wolf island, basal area (m^2/ha) of trees based on all stems over 15 cm diameter for the three large tree species (*Tsuga heterophylla*, *Picea sitchensis*, *Thuja plicata*), number of *Vaccinium* stems/m^2, and total biomass per ha of shrubs. The last two represent possible indices of "hide cover." Because the wolves range freely over the entire collection of islands (i.e. are global predators), the deer can choose islands based on (for example) protective cover or distance from Prince-of-Wales island, but not on the basis of whether wolves are there or not. Thus, any impact of wolves would be expressed via the non-predative mortality term, MORT.

Independent analysis of crude protein, neutral detergent fiber, acid detergent fiber, lignin and insoluble

ash content showed *V. parvifolium* to be the most nutritionally beneficial food (Kirchhoff, 1994). Indeed, Kirchhoff found this species to be the preferred food. Blueberries (*V. alaskensis* and *V. ovalifolium*) also are eaten. Although salal (*Gaultherium*) is an important food for deer elsewhere, this and the other shrubs were seldom eaten by animals in this particular population. In many areas in Alaska, overstory, as indirectly indicated by summed tree basal area, might be expected to bring winter relief from deep snows. The study area has low snowfall, so the effect is likely to be present but small.

For INTASS analysis, sample size was only 94; three of the islands had incomplete data. Eleven variables were involved. A survey of secondary effects showed that the impact of deer and physical factors on BRTH lowered var(ρ) by more than 50%. These secondary factors, therefore, were included, even though their inclusion brought the total number of coefficients to 17. Given the previously suggested statistical rule of thumb, a minimum of 5 and ideally at least 10 quadrats per variable, this means that while found values may differ significantly from zero, power of the level II steps undoubtedly suffers. The results are shown in Table 2.

In accordance with Kirchhoff's conclusions, INTASS clearly and unambiguously identifies *V. parvifolium* as the most valuable food. Indeed, the other foods appear to interfere with the value obtained from this species. After first level competition (α_T) is accounted for, there is an additional, secondary reduction of BRTH by deer density. Inasmuch as linear density feedback is accounted for already by the alpha term, this indicates an increasing rise in feedback intensity as the number of deer increases. Secondary effects of foods and physical factors on BRTH were sufficiently small that they were not incorporated into the final analysis.

Mortality rises with island area and falls with effective island area. One can only speculate here that larger islands are more likely to draw wolves, while the fractionation of the land makes escape from them easier. Swim distance clearly reduces mortality, as expected, as do basal area, and both estimates of hide cover. Because basal area also may serve as an indicator of hide cover, these results are not surprising. Second level analysis indicates a more than linear increase in mortality with BRTH, i.e. with conditions positively impacting BRTH. This is consistent with Kirchhoff's observations that deer occupying island with high food availability (those close to Prince-of-Wales Island) also incur more mortality from wolves. Finally, mortality drops with increasing deer density, all else being equal.

Other than agreement with independently derived conclusions, the results of the INTASS analysis might be tested by re-running the analysis on either another set of islands or a subset of the islands used here, but with some specified difference in (say) management history. Unfortunately there is no such alternate or specified subset.

7.2. Plants

An example of applying INTASS to plants comes from work we've been pursuing at the Desert Experimental Range in southwestern Utah. This is a large area of high desert set aside in 1933 for research on grazing impacts. Various paddocks, each approximately a 0.6 km × 1.2 km, have been grazed consistently during the same season and by the same number of sheep every year since 1934 (for more detail, see Emlen et al., 1989; Freeman and Emlen, 1995). Cheat grass (*B. tectorum*) was sampled using 10 cm diameter circular quadrats (slightly larger than crown or root diameter) in the spring of 1997, at the time seeds were ripening. As a cleistogamous annual grass, cheat grass fitness can be defined unambiguously as the number of seeds produced per seed, and the seed can serve as the "individual." Thus, if n was the number of seeds on the targeted parent plant in a given quadrat, that quadrat was entered n times in the INTASS calculations. Other variables described soil chemistry (phosphorus, nitrate, total and exchangeable potassium, exchangeable calcium, magnesium and sodium, and ammonia), all in parts per million, percent cover of cheatgrass and each of the other plant species, grazing intensity (0 for none, 1 for 2500 sheep days, 2 for 3750 sheep days and 3 for 5000 sheep days per paddock) and degree of development of the cryptogamic crust (mosses and lichens, subjectively scored as 0, 1 or 2). Physical factors included pH, percent organic matter, electroconductivity, percent bare ground in the quadrat and small mammal activity both within the quadrat and outside the quadrat but within 1 m of the target plant. All soil constituents were included as potential nutrients in the

Table 2
INTASS results for Alaskan deer

Variable	Per-quadrats mean	Per-individual mean	
Foods (kg/m^2)			
(1) *V. parvifolium*/10	1.647	2.953	
(2) *V. alaskensis* and *V. ovalifolium*	6.301	7.340	
(3) Summer forbs	6.812	8.712	
(4) Winter forbs/10	2.220	2.298	
Target species number per island			
(5) Deer (via pellet group density)	1.102	1.855	
Physical variables			
(6) Island size (ha)	4.618	2.894	
(7) Effective island size (ha)	4.268	5.859	
(8) Swim distance (km)	1.098	1.421	
(9) Basal area (m^2/ha)	1.859	1.921	
(10) No. of *Vaccinium* stems	2.890	3.002	
(11) Total shrub biomass	1.932	2.212	
Coefficient	**Estimated value**	**Standard deviation**	***t*-value**
BRTH			
Food values			
v_1	0.00056	0.00011	5.283**
v_2	−0.00029	0.00036	−8.072**
v_3	−0.00037	0.00025	−14.677**
v_4	−0.00015	0.00075	−19.727**
Probability of utilization given encounter			
α	0.10000	0.0000	Fixed
Secondary impact of deer on BRTH			
ξ_{B_5}	−0.09505	0.00141	−67.379**
MORT			
Importance of physical factors to MORT			
ξ_6	0.0017	0.00008	22.2910**
ξ_7	−0.0048	0.00007	−70.1218**
ξ_8	−0.0485	0.00050	−97.9495**
ξ_9	−0.0484	0.00061	−79.4171**
ξ_{10}	−0.0017	0.00020	−8.6666**
ξ_{11}	−0.0041	0.00016	−25.4186**
Secondary impact of deer on MORT			
ξ_{M5}	−0.03516	0.00176	−19.9815**
Secondary impact of BRTH on MORT			
ξ_{MB}	3.29346	0.00000	Huge**
γ_{MB}	11.91026	2.35677	5.0536**

Mean fitness = $(\beta - 0.1496) - (0.0000) - (\mu - 0.151)$. Variance fitness = 0.0027.
** $P < 0.01$.

BRTH term, although sodium is likely also to be a physical factor via its effect on soil moisture availability. Four subsites were used: an ungrazed area, and lightly (9.6 animal days/ha), moderately (19.2 animal days/ha) and heavily (28.8 animal days/ha) grazed areas. The three latter areas had been grazed in late fall, consistently for 62 years, and so constitute a long-term manipulation experiment. Thus, successful prediction of cheatgrass cover in randomly distributed quadrats in one of the subsites, based on a model derived from plant-targeted quadrats in the other three would be strong verification of the model's predictive power.

Impacts of various nutrients and physical factors on a plant species depend very much on both geographic location and plant adaptive history. Therefore, an assessment of INTASS accuracy based on comparison with data in the literature must be made carefully. Nevertheless, a few findings seem a propos. DeLucia et al. (1989) found phosphorus deficiency to reduce growth and vigor in *B. tectorum* in their Great Basin studies, suggesting it is a limiting factor (at least at this study site). Woodward et al. (1984) concur. Klemmedson and Smith (1964) suggest that small mammal activity (in their case *Microtus montanus*) might delay succession from cheatgrass cover to subsequent, perennial plant species. If this is true also at the Desert Range (a quite different suite of small mammal species), we should expect to find either a positive effect of small mammal activity on BRTH or a negative effect on MORT. Young and Evans (1985) report that bromus generally does not germinate well on bare ground, but needs a certain amount of litter or mulch. Thus, bare ground cover should exert a negative influence on BRTH or a positive influence on early survival. Finally, Tausch et al. (1994) found that fall clipping (simulating grazing pressure) enhanced cheat grass production. Sheep grazing, then, at least at some level of intensity, should have a positive impact on BRTH.

We obtained data for targeted plants from 157 quadrats. Although "individuals" are represented by a considerably larger number of seeds, independent, associated data come from only the 157 quadrats. Therefore, sample size is 157. A preliminary survey of these data showed cheatgrass to occur only or almost only with three other species, and with those three in fewer than 10% of the quadrats. Accordingly, in the interests of holding down the number of variables, the only plant considered in the analysis was cheatgrass itself. The analysis thus included eight soil nutrients, one plant species, one grazer (sheep) and six physical variables. Secondary effects of nutrients on BRTH significantly lowered var(ρ) and were included in the final analysis. Results are given in Table 3.

According to the analysis, the usually critical nutrients, P, NO_3–N and NH_4–N not unexpectedly enhance BRTH. Potassium's effect is mixed; total K appears beneficial to BRTH, exchangeable K appears to have a negative effect. Magnesium is detrimental (perhaps interfering with uptake of other nutrients?); sodium is beneficial. Secondary effects on BRTH include

Table 3
INTASS results for *Bromus tectorum*

Variable	Per-quadrats mean	Per-individual mean
Soil nutrients (ppm)		
(1) Phosphorus	12.244	12.401
(2) NO_3–N	4.921	5.485
(3) K-total	2.991	3.074
(4) Ca-ex	71.339	68.456
(5) Mg-ex	5.955	5.729
(6) K-ex	5.724	5.728
(7) Na-ex	33.379	37.414
(8) NH_4–N	5.536	5.592
Plant species—cover (%)		
(9) *Bromus tectorum*	3.188	4.716
Grazing intensity—0, 1, 2, or 3		
(10) Sheep	1.490	1.335
Physical variables		
(11) Mammal activity inside quadrat	0.032	0.0389
(12) Mammal activity outside quadrat but within 1 m	0.252	0.300
(13) Percent organic matter	0.773	0.822
(14) pH	8.012	8.034
(15) Electroconductivity	0.541	0.569
(16) Bare ground cover/100	0.840	0.807

Table 3 (*Continued*)

Coefficient	Estimated value	Standard deviation	*t*-value
BRTH			
Nutrient values			
v_1	0.0196	0.01774	1.106
v_2	0.1349	0.00705	19.118**
v_3	0.3241	0.00805	40.240**
v_4	−1.1691	0.03694	−31.645**
v_5	−0.6441	0.01490	−43.238**
v_6	−0.2243	0.01016	−22.081**
v_7	0.1318	0.00443	29.785**
v_8	0.5183	0.01467	35.343**
Competition			
α_T	0.001	–	Fixed
Secondary effects of nutrients on BRTH			
ξ_1	0.0002	0.00117	0.160 (NS)
γ_1	0.0001	0.00000	1.936**
ξ_2	−0.0080	0.00115	−6.948**
γ_2	−0.0001	0.00008	−0.962 (NS)
ξ_3	0.0170	0.00426	4.005**
γ_3	−0.0009	0.00036	−2.497**
ξ_4	−0.0293	0.00045	−64.679**
γ_4	0.0002	0.00000	62.659**
ξ_5	0.0317	0.00232	13.657**
γ_5	−0.0007	0.00013	−5.413**
ξ_6	−0.0386	0.00246	−15.673**
γ_6	0.0009	0.00008	11.769**
ξ_7	−0.0004	0.00008	−5.429**
γ_7	0.0000	0.0000	3.247**
ξ_8	−0.0111	0.00121	−9.175**
γ_8	0.0007	0.00007	10.029**
Predation			
δ_{10}	−0.3397	0.00604	−56.228**
Other mortality			
ξ_{11}	0.7532	0.01544	49.737**
ξ_{12}	0.1949	0.01483	13.138**
ξ_{13}	0.1814	0.01293	14.033**
ξ_{14}	0.6227	0.02268	27.449**
ξ_{15}	0.6164	0.02591	23.788**
ξ_{16}	−0.0432	0.02856	−1.513 (NA)

Mean fitness $= (\beta + 0.0985) - (-0.4535) - (\mu + 5.5548)$. Variance fitness $= 0.0569$.
** $P < 0.01$.

positive influences from P, Ca and NH_4–N, and negative influences from NO_3–N. Thus, the negative influence of Ca and the positive influence of sodium are somewhat mitigated at higher concentrations, the positive effects of P and NH_4–N build with concentration, and the value of NO_3–N declines. A negative secondary impact comes from total K, indicating that its primary effect is diluted at high concentrations.

As found also by Tausch et al. (1994), grazing appears to have a positive impact on fitness, perhaps by stimulating growth or thinning the population. Small mammal activity, whether directly adjacent to the plants or in the near vicinity, is detrimental to survival (or to BRTH). This is contrary to the suggestion of Klemmedson and Smith (1964). On the other hand, theirs was only a suggestion, not an observation, and

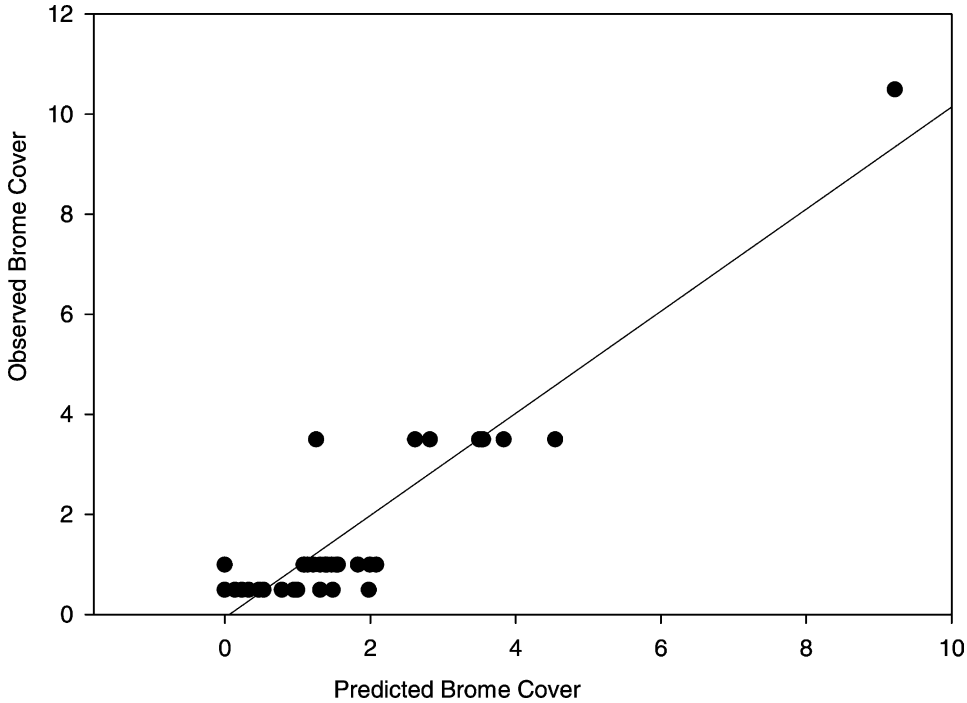

Fig. 1. Observed vs. predicted cover of *Bromus tectorum* in one paddock based on an INTASS expression derived with data from three other paddocks with different long-term grazing histories.

we are dealing with an entirely different set of small mammals at the Desert Range. Percent organic matter, pH and electroconductivity also negatively impact survival. Bare ground appears to lower mortality, though the effect is not statistically significant.

7.2.1. Validity test

The above comparisons to existing findings (and common sense) provide only limited (and questionable) validation. However, recall that the grazing history at the Desert Range represents a thoroughly controlled, long-term experiment. Therefore, an accurate prediction of cheatgrass cover in one paddock (one grazing history) based on model parameterization from data gathered in the others (alternate grazing histories) would provide strong support for the predictive accuracy of INTASS. In this case, the model, parameterized using data from three of the plots (grazing intensities 0, 1, 3) was applied to predict cheat grass cover, quadrat-by-quadrat, in the fourth plot (grazing intensity = 2), given the quadrat-specific values for the other variables. The reader is referred to Fig. 1. Slope of the line is 1.093 ± 0.106; if the one high point is deleted, the slope becomes 0.817 ± 0.072, suggesting possible undermatching.

8. Discussion

8.1. Quadrat size

In Section 1, we ignored the likelihood that the environmental input determining an animal's behavior, or a plant's success, comes via signals operating at more than one spatial scale. But a nocturnal mouse might respond to highly local visual signals, scents coming from farther off, and auditory information arising from anywhere up to many meters away. A plant's reproductive success may depend on competitor conditions extending no farther than its own crown or root mass, but also on soil conditions over a larger area and on grazers whose likelihood of eating

it depend on physical environmental factors at a still greater spatial scale. It should not be surprising, then, to find that different variables exert their maximum effects at different scales (see, e.g. Vail, 1993; Debouzie et al., 1996), or even that the effects of a variable change may have opposite impacts at different scales (L. Freidenburg, personal communication) Consider, for example, a fish that positions itself in a stream according to current velocity, substrate, density of vegetation overhanging the banks, and the density of conspecific competitors. Suppose the physical variables define a sensory/responsive world extending three meters about the fish and that the experimenter, accordingly, uses 3 m radius sampling units. The effects of the physical variables on fitness, then, may reasonably be defined by an INTASS analysis. If the conspecific interactions take place within a space of, say, 1 m, however, evaluation of their impacts on fitness are likely to be mismeasured or even missed entirely. Indeed, any model that ignores scale, or ignores the potential need to incorporate data at more than one scale could be seriously misleading (Hanski, 1991).

Of course, if expected fitness values converge over small quadrats, fitnesses in large quadrats, being the means of fitnesses in their component smaller parts, must also converge (unless unoccupied, inappropriate microhabitats are a part of the larger quadrats). Thus, choosing only the larger quadrat size need not lead our experimenter seriously astray. On the other hand, response to the mean environmental variable values represented in a mixture of smaller regions means that the derived parameter values are likely to be of smaller magnitude and have larger confidence intervals. Accordingly, we suggest that any INTASS analysis make use of a range of scales by utilizing information from nested quadrats. One rule of thumb: Avoid quadrats large enough to encompass non-panmictic areas or source-sink habitats (Morris, 1995, 1989; see Section 8.3).

8.2. Global fluctuations

Weather variables and highly mobile predators may act on a species at such a large spatial scale that their values are effectively constant over the study area. For example, mice cannot very well avoid foxes directly, although they can choose surroundings distasteful to foxes. When data are collected at repeated intervals, variations in these variables may be incorporated directly into the analysis. However, if data are collected only once, though these variables may be important determiners of fitness, they contribute nothing directly to the analysis.

8.3. The landscape level and source-sink situations

When a study site includes different *macro*-habitat types, as in applications at the landscape level, the assertion of equal expected fitnesses need not hold (Morris, 1995, 2002, 1989; Ostfeld and Klosterman, 1986). For example, in a site that incorporates both fields and scattered woodlots we could not, a priori, assume that woodmice inhabiting both would nevertheless be equally fit in both. In such cases, we are faced with a source-sink situation in which the population in one habitat is maintained by virtue of dispersal from the other. In such circumstances it would seem that INTASS could not be applied, and yet if the methodology is to be useful, it must ultimately be applicable at a landscape level. The problem, actually, is quite easily circumvented. Unless the habitats are quite different, the expressions for BRTH, PRED and MORT should be very similar. Thus, the complication can be dealt with simply by approximating mean fitness deviations among habitats as an expression of deviations from habitat-specific variables, and appending the expression to the fitness model:

$$\begin{aligned}\rho &= \mathrm{BRTH} - \mathrm{PRED} - \mathrm{MORT} - \mathrm{COR} : \mathrm{COR} \\ &= \sum \theta_n X_n + \text{constant}, \end{aligned} \tag{12}$$

where $\{X_n\}$ refers to environmental variable values measured at the macro-habitat scale (or approximated as means of certain variables calculated over quadrats within each macro-habitat). This correction term might be used also in cases of population cycles, where there are reasons to suspect that different sites represent different stages in the cycle. Inasmuch as cycle position can be determined from ratios of the species' populations involved, deviations from the mean ratio might be used as variables in the correction term. Where this calculation is needed, it should be carried out as part of the first step in analysis (see above) so that fitnesses are equaled among macro-habitats. In practice, it is convenient to incorporate $\{X_n\}$ into $\{Z_m\}$ and append COR to MORT.

If the habitats are sufficiently different to indicate divergent forms for BRTH, PRED or MORT, INTASS should be carried out separately for each such habitat.

8.4. Applications

INTASS, as presented here, should prove useful in unraveling the web of interactions among species and between species and aspects of the physical environment. In doing so, it should prove useful also in generating testable hypotheses about the nature, intensity and causes of these interactions. Practically, it should prove useful in providing critical information about essential habitats for threatened and endangered species, and about the specific conditions under which exotic species successfully invade and maintain themselves, or ultimately fail. When based on data over time, so that global variables can be incorporated directly, it has great potential as a predictive tool. Currently, projecting the long-term consequences of management actions or global change is more an art than a science. Despite the existence of a myriad of models and associated software, our predictive capabilities remain limited. Accurate evaluation of a community's dynamics requires site and time-specific data and their incorporation into dynamic models complex and complete enough to portray a plethora of interactions accurately. When the basic assertion of equal ρ is met, INTASS is an approach that may meet these criteria.

As constructed, consistently using coefficients with clear biological meaning, the INTASS model makes it possible for an investigator to read off directly the effect of any variable, biotic or physical, on a target species' fitness (level I analysis). Secondary effects on the level I coefficients also can be read off directly from the results of the higher level analyses.

Finally, even though animals may not have the capability of detecting, much less reacting appropriately to anthropogenic stressors such as contaminants, their populations certainly must respond at the macroscale. Thus, such stressors can be incorporated into the COR term in an INTASS analyses. Inasmuch as more than one stressor can be dealt with, as well as secondary effects of, say, physical factors on the fitness effects of those stressors, INTASS may prove a useful tool for dealing with multiple stressors.

How does INTASS relate to other population/community modeling approaches: Most such models can be classified either as extremely general, bookkeeping constructs, such as the logistic, Ricker or Beverton-Holt equations, or as parameter-driven, species- and situation-specific expressions. Anyone involved in applying models will be familiar with the latter; recent examples from this journal include Xie et al.'s (1999) exploration of white-tailed deer and Bartholow's (1996) treatment of salmon. Individual-based models fall into this category. Another class of models, so-called structural-dynamics models (see, e.g. Nielsen, 1992; Jorgensen, 1992), have the capacity, at least in theory, to use emergent ecosystem properties to update parameter values as they change over time. Such approaches take cognizance of the probability that as populations (and other environmental conditions) change, the nature of their interactive dynamics changes also, and use "goal" function such as the maximization of energy (see Jorgensen, 1992) to progressively update the underlying models over time. INTASS, in using the emergent property of spatial distribution to determine model parameters fits into this last category. Although, as it stands, it is meant primarily as a tool to explore interactions, suggest hypotheses and predict the stable (central tendency) consequences of environmental manipulations, it can, with additional information on the actual numerical values of fitnesses, be used to simulate dynamics. Might Jorgensen's energy maximization idea be used to update parameter values over time in such simulations? Possibly; so far this has not been tried.

As with any model-constructing protocol, problem situations will arise; the reader can undoubtedly envision all manner of caveats to the successful application of INTASS in some circumstances. We address two important caveats in Appendix B.

9. Conclusion

Current goals in ecology include the control of invasive species, the identification of essential habitats for threatened and endangered species, and predicting the consequences of management actions, contaminants and global change. Toward these ends grizzled guru naturalists have held wetted, prognostic fingers to the wind, ecologists have elaborated on such classic tools as the logistic, Ricker and Leslie

matrix equations, and systems modelers have constructed elaborate mathematical simulations. A difficulty common to all these approaches, except arguably the first, is that adequate consideration of all the various interactions involved—competitive, predative, synergistic and physical-biotic—and the modifying effects of any one set of such interactions on all the others, involves knowledge of a great number of coefficient values many of which are not easily obtainable. And in complex systems, small errors tend to beget larger errors. In this paper we have presented a model that we feel encompasses sufficient biological detail for use as a predictive tool, and have provided a means by which its coefficients can be obtained from field data without the need for manipulation experiments or destructive sampling. The data gathered for this purpose for any one species, moreover, can be used for parameterizing the model for other species, thus enabling us to generate simultaneous dynamic equations for community simulation while conserving time, effort and funds. We recognize that the assertion upon which the approach rests may prove unsupportable in many instances. Nevertheless, the useful information to be gained when it holds is sufficiently important to warrant serious consideration. Ultimately, its truth and efficacy can be determined by tests of the INTASS method itself.

Appendix A

The efficacy of INTASS relies on the presumption that expected individual contributions to fitness tend toward equality. We argue that this condition is approximated in many cases, and that in others, deviations might often be corrected for.

The IFD, as usually interpreted, states simply that organisms, given the freedom to choose their surroundings, distribute themselves in proportion to the availability of resources. A considerable body of data supports, or purports to support this claim when patches are small and interconnected (Kluyver and Tinbergen, 1953; Brown, 1969; Fretwell and Lucas, 1970; Parker, 1970, 1974; Grant, 1971; Fretwell, 1972; Milinsky, 1979, 1984; Witham, 1980; Gass and Montgomerie, 1981; Goss-Custard, 1981; Grubb and Greenwald, 1982; Harper, 1982; M'Closkey, 1982; Maynard Smith, 1982; Godin and Keenleyside, 1984; Power, 1984; Sutherland and Parker, 1985; Parker and Sutherland, 1986; Recer et al., 1987; Houston and McNamara, 1988; Croy and Hughes, 1991; Wahlstom and Kjellander, 1995; see also Taylor, 1975, 1976; Brew, 1984, Morris, 1989, and the discussion in Emlen et al., 1989). See also Harper and Gajic (1961), Palmblad (1968), Harper (1977), and Freeman and Emlen (in preparation). However, some of the above articles also report poor fits and note, generally, a bias toward the over-utilization of poorer resource patches (see the review table in Tregenza, 1995; see also Zach and Smith, 1981; Marshall and Frank, 1995, and the review by Abrahams, 1986, but see Bautista et al., 1995).

Consider the bias first. Does it negate the concept of IFD? If distribution is to be predicted solely on the basis of available resources, the answer almost surely is yes, for the factors governing animal distributions certainly extend beyond just food (Kacelnik et al., 1992; Abrahams, 1986; Grand and Dill, 1999; Lima and Dill, 1989). Indeed, it must be fitness, per se, the integrative effects of food and all other factors impinging on growth, reproduction and survival, that ultimately determines dispersion. The question, therefore, needs rephrasing: if we define the IFD as an equalization of fitness, based not only on resources, but on all factors impinging on fitness, do the data support it? Sih (1980, 1982) has shown that a foraging aquatic insect balances risk from predation against food richness in such manner as to equalize rate of food intake across food rich and food poor patches. Because mortality over the period of such matching is very low, equal food intake rates translate closely to equal fitnesses. Tyler and Gilliam (1995), in an experiment with stream fish, show good fits to predicted dispersion when energy costs of maintaining position in a current, in addition to resource availability (i.e. total, net energy balance), are considered. Korona (1990), discussing the role of cost in moving among patches, notes that where cost was low, his flour beetles (*Tribolium*) fit an IFD quite well. Bernstein et al. (1991), working with a model system, show that theoretical fits to a classical (resource-based) IFD are quite good if both travel costs and interference effects are low. An excellent discussion of both cost and interference is provided by Kennedy and Gray (1993). In light of these observations, it seems appropriate to conclude, with Abrahams (1986), that "what appears to the

observer as a departure from IFD may actually be a perfect IFD from the animals' perspective." That is, if cost of movement is small (as it should be between patches of the small size we recommend for quadrats), and if all factors impinging on fitness are considered, animals should distribute themselves such that fitness (*not* necessarily equivalent to resource input) is equalized across patches.

Unfortunately, difficulties remain. In addition to the consideration of measurable environmental factors other than food availability, poor fits can be generated by overlooked factors. For example, Hugie and Dill (1994), using a simple three-trophic level model found, when both prey and predator were allowed to choose their surroundings, that the race between prey seeking safety and predators seeking sustenance resulted in a prey distribution independent of the number of predators. Simply noting a difference in the spatial and/or temporal scale of habitat choice by the two species would have altered this finding. Note also the study of Inman (1990) with starlings in which he looked at the probability distribution over time of individuals in the better of two patches. On average, the better patch was occupied about the predicted proportion of time, but the distribution showed far more cases where birds crowded into one or the other patch than expected. Flocking behavior clearly affected the results. This latter work demonstrates not only the importance of including all fitness-affecting factors in a model, it also points out an important and usually neglected aspect of experimental tests of the IFD. Animals may have evolved behavior, reflecting adaptation to natural conditions, which persist even when the experimental set up does not call for it. To the extent this occurs, any predicted dispersion pattern must be erroneous.

To some extent, neglect of unanticipated factors affecting dispersion can be dealt with by using models that incorporate multiple secondary effects. But we cannot rely on this approach alone, for even slight differences among models may lead to marked differences among predicted dispersion patterns (Van der Meer and Ens, 1997). Clearly, this presents a problem for those wishing to apply the IFD. Interestingly, though, while the effects of slightly different model forms are amplified when a presumption of equal fitnesses is used to predict dispersion, the reverse does not hold; when dispersion patterns are fed in to the various models to predict fitnesses, differences are quite small. That is, predicting fitness from distribution data is a much more robust process than predicting distributions from equal fitnesses. INTASS, inasmuch as it uses distribution data to parameterize a model under a presumption of equal fitnesses should, therefore, be buffered from this problem. Proof of the pudding, of course, comes when the parameterized model is tested by predicting dispersion patterns in independently sampled quadrats (see Fig. 1).

Unequal competitive ability can contribute to poor fits (Sutherland, 1983; Sutherland et al., 1988; Inman, 1990). "Unequal competitors" translates to "different phenotypes." If there exist no differences in habitat preference among such phenotypes, then no difficulties arise (Grand, 1997), for each phenotype can, on its own, be expected to disperse itself such that expected individual contributions are equal (Hugie and Grand, 1998; though see Grand and Grant, 1994). But if the different phenotypes exhibit different habitat selection, the assertion of equal ρ-values will not be met. Sutherland and Parker (1985) and Parker and Sutherland(1986) have suggested that if each competitor is assigned a competitive weight relative to its success in finding and obtaining resources, that the IFD still holds, only in terms of summed weights inhabiting a patch rather than the number of individuals per se. In some cases at least, this weighting approach works (Sutherland et al., 1988; Grand, 1997; Grand and Dill, 1997). Unfortunately, it does not bail us out for purposes of INTASS, for while expected fitness per unit weight may tend toward uniformity among patches of microhabitats, fitness per individual need not do so. The problem is exacerbated by despotism, where certain individuals restrict the movements of others.

Occasionally, unequal competitive ability leads to disjunct habitat use. Dominant and subordinate male redwing blackbirds, for example, may occupy quite different habitat in springtime; salmon fry, depending on their size, may spend their time in stream main channels or side channels. In such cases, the problem is rendered moot; we simply treat the population as two separate "species." And where, as in both of these examples, the different habitats represent a source and a sink, we may apply the correction presented in Section 8.3 of the discussion. If, as in most cases, though, the habitats overlap, we must make a different sort of correction. In this case, because the

differences in competitive ability likely relate to differences in individual characteristics, we may be able to incorporate these characteristics in a manner similar to our use of macro-habitat differences in correcting for source-sink situations. Secondly, these characteristics can be incorporated as modifiers of level I model coefficients in the same way that physical variables are used to modify BRTH and PRED. Where history, more than current characteristics of the individuals involved determine competitive ability, though, all bets are off.

Occasionally what we identify as a species is, in fact, a set of species. And sometimes, to keep the number of variables manageable, we may find it convenient to lump species into a single super-species (the genus *Carex* comes to mind). Either case results in a ρ expression that confounds the separate species functions into some kind of complexly weighted average. The situation, then, is the same as that for unequal competitors. So long as the individual functions are similar, such practice still provides a reasonable description of what makes the conglomerate species tick. Where the functions are likely to differ significantly, it will be better to treat each entity on its own. This situation can arise even within a species, where significant differences in life style may follow from differences in life stage, size, age, sex, or phenotypic morph. Indeed applications of INTASS to different morphs may be useful in exploring the environmental causes for balanced polymorphisms or the reasons for deviations from genetically predicted sex ratios.

No equalization of fitness can come about in the absence of adequate environmental information (Abrahams, 1986; Kennedy and Gray, 1993; Ranta et al., 1999). A paucity of information can arise from the indirect effects of dominants on subordinates' ability to sample their surroundings (Abrahams, 1986), because of a need for snap decisions forced by the imminent presence of predators (Gilliam and Fraser, 1987), from limited memory capacity, or from spatial and/or temporal environmental unpredictability (Grand and Grant, 1994). Tyler and Hargrove (1997) present a dispersal model incorporating functional response (type II), a marginal-value theorem patch departure rule, limited memory of surroundings and environmental patchiness (expressed as a fractal dimension), and find that fits to the IFD are good if memory is long and movements are large relative to environmental grain. Fit falls off drastically as these values decline. These results make the need for good environmental information obvious. The bad fits generated by Tyler and Hargrove's model are likely to be alleviated if individuals, rather than simply moving periodically to some new patch, are allowed to sample patches as they go. Finally, a need to explore ones' surroundings to gain the information necessary for IFD (Emlen and Emlen, 1975; Royama, 1970; Goss-Custard, 1981) leads also to such "overuse" of poor habitats. However, presuming that such exploration (and simple, passing through movements) represent the vast minority of observations, their influence, likewise, should remain minimal. Errors arising from inappropriately including poor habitat quadrats can be minimized if those quadrats containing only very few individuals are dropped from the analysis.

It is clear that an individual's responses to its immediate surroundings must depend on its physiological (and psychological) state and, therefore, on its history. Ideal dispersion behavior can be modeled in light of ongoing histories and experience, using a dynamic programming approach (McNamara and Houston, 1990). By such standards our model, extensive as it is in many respects, remains hopelessly simplistic. However, we make no pretense of accurately modeling individual responses; our appeal is to the expected behavior of all individuals, jointly considered, momentarily occupying a given microhabitat. We look at our approach as a kind of statistical mechanics approach to McNamara and Houston's *n*-body problem.

Finally, we stress Morris' (2002) admonition about the efficacy of IFD when Allee effects occur. Only above the threshold value at which density-dependence becomes negative can we expect our assertion to hold. Morris' isodars might be used to assess whether an Allee effect occurs and, if so, where the critical density lies. When in doubt, the user might try running the analysis deleting the most sparsely populated quadrats. If problems occur, they should show up in a scatter of points near the origin on test graphs.

The upshot of the above discussion, at least when unequal competitors do not show distinct differences in microhabitat preferences, and when movement rates are on a spatial scale similar to or larger than environmental patchiness as viewed by the species of interest, is good support for reasonable fits to the IFD (generalized to fitness, rather than simply resource

acquisition). That is, we can expect individuals to distribute themselves so that their expected contributions to fitness approach equality among occupied microhabitats. We note also that it may be possible to compensate for deviations from the IFD by including in the analysis measures of individual characteristics.

Appendix B

B.1. Temporal considerations

Fitness, as defined here for animals, is an instantaneous rate. As such, its value almost certainly changes from season-to-season, night-to-day, or even hour-to-hour, as may the values of some of the variables to which the animals respond. Therefore, a full understanding of the factors influencing average fitness over time can follow only from data gathered over time as well as space. In this regard, note that ρ-values are additive. Therefore, we could analyze sets of data gathered at different points in time and simply add the resulting expressions for ρ. This approach has its hazards, though. Because the INTASS analysis gives fitness only as a proportional value, adding ρ-values will give meaningful results only if each element in the sum can be appropriately weighted (i.e. approach has its hazards, though). Because the INTASS analysis gives fitness only as a proportional value, adding ρ-values will give meaningful results only if each element in the sum can be appropriately weighted (i.e. relative to its time-specific contribution). These relative contributions are not always known or easily determined. An alternative approach is to gather information at different times (presumably on a stratified random basis) and perform the INTASS analysis on the lumped data. This approach, by analyzing the response of individuals occupying hypothetical, time-averaged quadrats, circumvents the above problem. It has another advantage as well. Animals, in fact, almost surely maximize their fitness contributions by responding in mixed fashion over time. By presuming an animal at a water hole has equal instantaneous fitness to another that's sleeping, or still another feeding, would almost surely be inappropriate. It is the behavior of an animal averaged over a day that determines its fitness contribution for that day. Accordingly, we recommend that animal data be gathered throughout the day, that quadrats randomly drawn from sets collected in one given time frame be averaged with—or appended to—similarly drawn quadrats from each other time frame, and that these compound quadrats be used to represent hypothetical individuals in INTASS analysis.

B.2. Incomplete sampling by the biologist

As with any fitting procedure, the neglect of one independent variable can impact the estimated contribution of another. Thus, the value of the biologist's insight into surmising, a priori, what variables are likely to affect fitness cannot be overstated. Can the effect of a habitat change on a population of deer mice be reasonably ascertained without data on the flea species parasitizing those mice? How accurately and how reliably can the dynamics of a plant community be simulated without consideration of local soil chemistry, or without data on specific groups of myccorhizal fungi? Studies are currently underway to determine the answers to such questions in desert plant communities.

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