

CHAPTER 7

GENERAL DISCUSSION

INTERFERENCE COMPETITION AND THE DYNAMICS OF POPULATIONS

This thesis deals with interference competition among foraging waders as a research topic in itself. In the General introduction, I argued (1) that although competition holds a prominent position in ecology, the process is as yet not well understood, (2) that a proper understanding of the phenomenon requires ideas on the mechanisms of competition and on the evolution of competition-related traits, and (3) that variation between individuals is essential to the mechanisms of competition and to the evolution of competition-related characteristics. This motivated me to study the mechanisms of interference competition among foraging waders. Other students of interference competition among waders have merely been interested in the consequences of interference competition for the dynamics of populations (e.g., Goss-Custard, 1980; Ens *et al.*, 1994; Sutherland, 1996). In this chapter I discuss the link between interference competition and the dynamics of populations. I will explain why I have not touched upon this link in my own research, and I will nevertheless suggest some new directions for further study.

WHY LINKING COMPETITION TO POPULATION DYNAMICS?

Why would students of population dynamics be interested in individuals? The various arguments that have been put forward can be categorized in three groups.

DISSATISFACTION WITH CLASSICAL MODELS OF POPULATION DYNAMICS

A first motivation stems from dissatisfaction with classical models of population dynamics (for a review of these models: see Hastings, 2005; for some examples: see Figure 7.1). These models assume that the dynamics of populations can be described in terms of a single state variable (population density; DeAngelis & Gross, 1992b). This presumes that individuals are all identical, or, if it is acknowledged that they are not, that the dynamics of the population can be described adequately in terms of the average individual (DeAngelis & Gross, 1992b). Additionally, it presumes that individuals are well-mixed, such that their density is the same everywhere, with every member of the population having an equal influence on every other member of that population (Durrett & Levin, 1994). Because of its analogy with physics, this approach can be referred to as the ‘mean field’ approach (Durrett & Levin, 1994).

The use of the mean field approach in classical models of population dynamics was motivated by the success of this approach in physics (Kingsland, 1995). A well-known example of a successful application of the mean field approach

The Pearl-Verhulst logistic equation

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right)$$

with; N : population density, r : per capita innate capacity for increase, K : carrying capacity

The Lotka-Volterra competition equations

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha_{1,2} N_2}{K_1} \right),$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - \alpha_{2,1} N_1}{K_2} \right),$$

with; N_i : density of species i , r_i : per capita innate capacity for increase of species i ,
 K_i : carrying capacity of species i , α_{ij} : inter-specific competition coefficient

The Lotka-Volterra predator-prey model

$$\frac{dN}{dt} = N (b - aP)$$

$$\frac{dP}{dt} = P (-d + kaN)$$

with; N : prey density, b : prey per capita birth rate, a : predator per capita capture rate,
 P : predator density, d : predator per capita death rate, k : predator per capita
 conversion efficiency

The Nicholson-Bailey parasitoid-host model

$$N_{t+1} = \lambda N_t e^{-aP_t}$$

$$P_{t+1} = c N_t (1 - e^{-aP_t})$$

with; λ : host reproductive rate, N_t : host density at time t , a : predator per capita searching
 efficiency,
 P_t : parasitoid density at time t , c : average number of viable eggs laid by a parasitoid

Figure 7.1. Four examples of classical models of population dynamics. Each of these models describes the dynamics of a population by a system of ordinary differential equations or difference equations, whereby the equations are unstructured: they do not account for between-individual differences in, for instance, size or age.

concerns the behaviour of gasses. In principle one might want to describe the behaviour of the whole gas in terms of the movements of all the gas molecules. As it turns out, however, the behaviour of gasses can very accurately be described in terms of the characteristics of the whole gas (Rosen, 1969; O'Neill et al., 1986; Laughlin, 2005). The key rationale underlying the mean field approach, thus, is that variation at the level of individuals averages out to yield highly constant statistical regularities at the level of populations, an idea referred to as collective exactness (Laughlin, 2005).

Dissatisfaction with the classical models of population dynamics originates from the growing awareness that individuals are unique and not mixed homogeneously (see for instance the papers in DeAngelis & Gross, 1992a). Violation of these assumptions is problematic whenever characteristics other than the mean are biologically relevant, or when the aggregated process is non-linear. Non-linearity is problematic for aggregation attempts because the average is not a good description of non-linear processes. Problems can also be expected when the aggregated process is stochastic (DeAngelis & Rose, 1992). In that case, the average may be a bad descriptor if the population size is small and/or if rare events have strong effects. Violation of the mean field assumptions can lead to qualitatively different predictions regarding the dynamics of populations (e.g., Lomnicki, 1988; DeAngelis & Rose, 1992).

Dissatisfaction with classical models of population in essence calls for an approach that accounts for variation between individuals. Any approach that wants to account for between-individual variation has to specify the extent to which it wants to do so but it also has to specify which characteristic of individuals is allowed to vary. Discussion about the first issue has been clarified by Metz and Dieckmann (1986), who identified three classes of models: p(population)-state models, i(individual)-state distribution models and i(individual)-state configuration models. P-state models do not account for differences between individuals. The classical models clearly fall into this class. I-state distribution models do allow individuals to vary; they describe the dynamics of a population by keeping track of the distribution of the characteristic(s) in which individuals vary. Leslie matrix models, for instance, account for variation in age by keeping track of the distribution of individuals over age-classes. I-state distribution models involve some aggregation (for instance, of individuals into age classes), but less aggregation than p-state models. I-state configuration models represent each individual as a separate, discrete, entity. They do not involve any aggregation. The second issue – specifying the characteristic that is allowed to vary – has attracted much less attention than the first one (Murdoch et al., 1992; van der Meer, 1997a). This issue is most apparent for i-state distribution models, where the number of characteristics is most limited. Age, sex, spatial position, size, reserves, nutritional status, behaviour, and genetics are all reasonable candidates that have featured in models of population dynamics. Although in many species (e.g., fish and invertebrates species) especially size will be a characteristic that is of importance for the dynamics of populations. Waders, however, reach adult size within weeks after birth so that size-differentiation is limited.

LINKING THE STUDY OF ANIMAL BEHAVIOUR AND POPULATION DYNAMICS

A second motivation springs from the realization that the field of animal behaviour and population biology have developed largely in isolation of each other. Students of animal behaviour have traditionally shown little interest in the con-

sequences of behaviour for the dynamics of populations. Students of population dynamics have concentrated on the mere determination of demographic parameters (such as population growth rate and carrying capacity) without much consideration on how these parameters result from the behaviour of the members of the population. This situation has led to several pleas for linking the fields of population dynamics and animal behaviour to each other (Hassell & May, 1985; Smith & Sibly, 1985; Goss-Custard, 1985; Sutherland, 1996).

Linking the fields of animal behaviour and population dynamics should enable the interpretation of population-level parameters in terms of the behaviour of individuals (i.e., the members of the population). Thus, the plea to do so essentially is a plea for more mechanistic detail to models of population dynamics. Indeed the advantages that linking the two fields should have are the advantages attributed to mechanistic models in general. First, mechanistic models are thought to be intellectually more satisfying than their phenomenological counterparts, because they (can) provide an understanding of how phenomena come about (e.g., Hassell & May, 1985; Smith & Sibly, 1985). Second, because of this understanding, it is also thought that mechanistic models can be extrapolated to novel conditions, or at least more so than phenomenological models (Sutherland, 1996). Third, because mechanistic models specify how the phenomena under study come about, they provide extra means to select among different models (namely on the basis of the assumed mechanisms; Smith & Sibly, 1985).

INTRINSIC ADVANTAGES TO STUDYING INDIVIDUAL ORGANISMS

A third motivation is found in the conviction that there are advantages intrinsic to studying processes at the level of individual organisms. Several arguments have been invoked to support this conviction. First, individuals are the organizational level upon which selection generally acts most strongly. Therefore, studying processes at the level of individuals provides the best possibilities to embed the study of population dynamics in the theory of natural selection (e.g., Smith & Sibly, 1985; Sutherland, 1996). Second, properties of individual organisms and the mechanisms by which they interact with their environment are measured relatively easily, because of the temporal and spatial scale at which they operate (e.g., Huston et al., 1988). Third, individuals, unlike units of other levels of organization, come in discrete entities, making individuals the most suitable organization unit (e.g., Łomnicki, 1992; Durrett & Levin, 1994). Fourth, the traditional ecological hierarchies all intersect at least at the level of individual organisms (MacMahon et al., 1978); this suggests that the level of individual organisms may be the most appropriate level to begin to explore commonality and integration in ecology (Pickett et al., 1994). The first of these arguments – that individuals are the organizational level that can be linked most easily to the theory of natural selection – leads to an approach to popula-

tion dynamics that accounts for between-individual variation, given that between-individual variation is a prerequisite for evolution by natural selection. The other three of these arguments imply an approach to studying population dynamics that is phrased in terms of characteristics of individuals.

HOW TO LINK COMPETITION TO POPULATION DYNAMICS?

Motivated by either of the above-mentioned arguments, several approaches have been developed that account for interference competition while studying the dynamics of populations ('interference-based approaches to population dynamics'). Three examples from the literature on waders are presented in Figure 7.2. The basic notions underlying these approaches are (1) that processes that determine population size may themselves depend on population size and (2) that interference competition may be the mechanism underlying density-dependence effects. These ideas are merged with the use of the ideal-free-distribution model of Fretwell and Lucas (1970). Based on the assumption that the spatial distribution of food is heterogeneous, this model predicts the distribution of animals over patches of food, while accounting for competition effects on intake rate.

Implemented in the study of wader population dynamics these ideas yield a framework with the following main ingredients. First, processes operating during the breeding season and those operating during the rest of the year are treated separately. During the winter, the main process of relevance for the size of populations is mortality. Mortality may have various sources, including predation, diseases and starvation. Population size is thought to affect mortality through density-dependent starvation. Starvation occurs when body mass (condition) falls below a minimum. Condition is determined by intake rate, which depends on population size through exploitative competition and/or interference competition. The essential relationships underlying these frameworks are 1) the relationship between population density and intake rate, 2) the relationship between intake rate and condition (body mass), 3) the relationship between condition and population density, and 4) the relationship between the population density in one winter and that in the next. At least in the framework presented by Goss-Custard, intake rate may also affect population size directly (a higher intake rate could lead to a reduction in the time spent on dangerous foraging grounds, and therefore in a lower mortality).

ARE ARGUMENTS MET?

To what extent do interference-based approaches to wader population dynamics acknowledge the various arguments to link models of population dynamics to the behaviour and/or the characteristics of individuals?

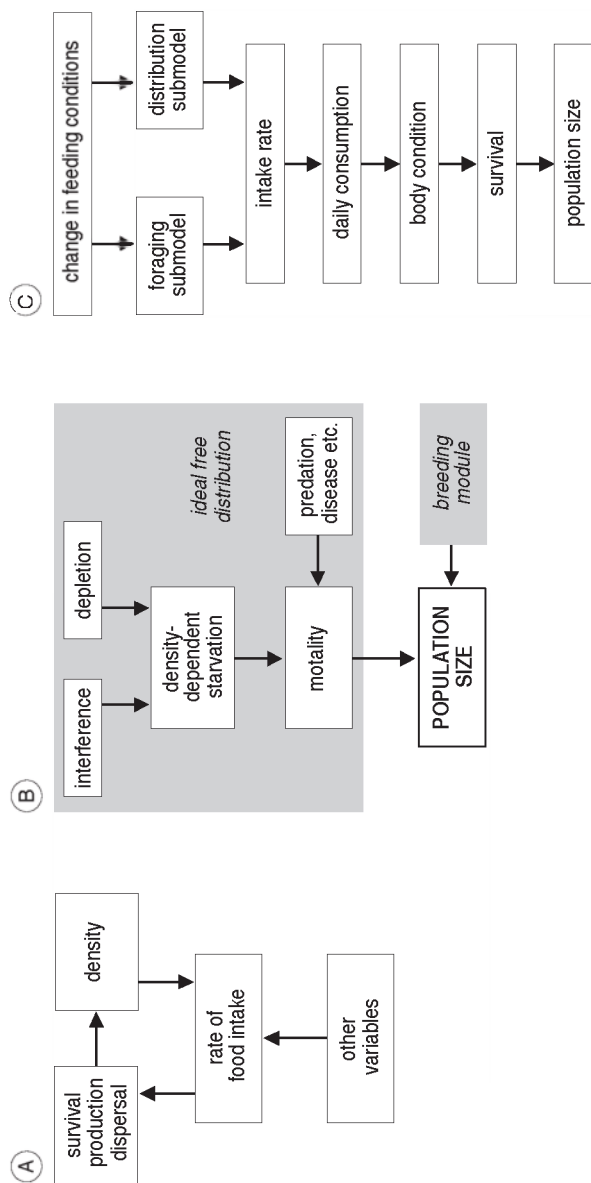


Figure 7.2. Schematic representations of the link between interference competition and population size in three examples. **A:** the feed-back loop for waders as explored in Goss-Gustard (1980). **B:** the framework for linking interference and depletion outside the breeding season with territorial behaviour in the breeding season to determine population size (from Sutherland, 1996; note that I inserted all processes relevant to breeding in the box 'breeding module'). **C:** flow chart showing how the behaviour-based model of Silliman et al. (2000) predicts the effect of the winter mussel food supply on the body condition of individual oystercatchers and on the starvation rates of the population. Although competition and the ideal-free-distribution model are not represented explicitly in this flow chart, both play an important role in the model: competition features prominently in the foraging submodel, and the rationale behind the ideal-free-distribution model forms the essence of the distribution submodel.

DISSATISFACTION WITH CLASSICAL MODELS OF POPULATION DYNAMICS

Critics of the classical models of population dynamics made a plea for accounting for between-individual variation. All studies that link competition among foraging waders to changes in wader population size use individual-based simulation models to do so, that is they use an 'i-state configuration approach'. This approach allows for a full account of between-individual variation. It has the advantage that technical difficulties as well as aggregation problems are avoided, but the disadvantage of limited generality (Caswell & John, 1992; DeAngelis & Rose, 1992). Furthermore, the fact that there is no limit to the number of variables that is allowed to vary in i-state configuration models often hampers a proper evaluation of model behaviour. It also makes the question as to which variables are allowed to vary less relevant. Therefore, let me consider the characteristics that should *at least* feature in interference-based models of population dynamics. The use of the ideal-free-distribution model implies that individuals should at least be allowed to vary in their spatial position. The assumption that density-dependence acts through starvation further implies that individuals should also be allowed to vary in condition (body mass). Perhaps surprisingly, however, in the absence of a third variable characteristic, it does not suffice to allow these two characteristics to vary. The reason for this is that according to the ideal-free-distribution model individuals all achieve the same intake rate, even though they vary in their spatial position. Therefore, individuals should be allowed to vary in at least one extra characteristic, the most obvious candidates being some characteristic directly related to the competition process, such as dominance status or competitive ability.

In modelling interference competition on itself (rather than its population dynamical consequences), analytical approaches have been used as well as simulation approaches. Van der Meer and Ens (1997) review six models of the generalized functional response. Applied in the context of the ideal-free-distribution model, these models only account for variation in the spatial position of foragers. Even though they all have a clear-cut interpretation in terms of the behaviour of individuals, they can be classified as p-state models in that they aggregate all individuals in a single state variable (forager density). Yet, some of these models of the generalized functional response have been extended to account for variation in dominance status (e.g., Sutherland & Parker, 1985; Parker & Sutherland, 1986), though this is often done in an *ad hoc* manner, whereby individuals are assumed to belong to certain competitive classes (but see van der Meer, 1997b). Such models could count as i-state distribution models, but they do not actually follow the distribution of individuals over the competitive classes. Instead, the proportion of individuals in each of the classes is assumed to be constant. Furthermore, all models that have accounted for between-individual variation in dominance status have made rather arbitrary decisions on how dominance relates to patch choice.

LINKING ANIMAL BEHAVIOUR TO POPULATION DYNAMICS

Above, I have argued that the plea for linking the fields of animal behaviour and population dynamics essentially is a plea for more mechanistic detail to models of population dynamics. In general terms interference-based approaches to wader population dynamics are indeed more mechanistic than classical models of population dynamics; they consider how the carrying capacity of a population comes about.

In more specific terms the interference-based approaches to population dynamics are all phrased in terms of the levels of organization concept, as is, for instance, apparent from the title of the book by Łomnicki (1988; *Population Ecology of Individuals*) and from the title of the book by Sutherland (1996; *From Individual Behaviour to Population Ecology*). According to the definition of mechanistic models of population dynamics as models that describe population dynamics in terms of the behaviour of individuals, interference-based approaches of wader population dynamics clearly are mechanistic. For the reasons presented in the first Reflection that follows on this General discussion, however, such may not be the most fruitful way to approach the topic.

Interference-based approaches to wader population dynamics are usually not phrased in terms of the process-rate definition of mechanistic models (as models that describe a phenomenon in terms of processes operating at a rate faster than that at which the phenomenon operates).

If mechanistic is defined as explaining how changes in population size come about while using parameters that are independently measurable, interference-based approaches to the study of population dynamics are not mechanistic. Even though mechanistic models of the generalized functional response exist (e.g., Beddington, 1975; Ruxton et al. 1992), all interference-based models of population dynamics use a phenomenological model, derived from an empirically determined relationship. Thus, all models contain at least one parameter that does not have a clear-cut mechanistic interpretation. This parameter is generally referred to as the interference coefficient ('mystery coefficient' would probably be a more appropriate reference to this parameter, given that it does not have a mechanistic interpretation) and is defined as the regression coefficient of the relationship between intake rate and forager density (several of the phenomenological models only differ in whether they apply log-transformation to intake rate, forager density or both). Although this interference coefficient may capture the interference effect, it does not specify how this effect comes about.

INTRINSIC ADVANTAGES TO STUDYING INDIVIDUALS

Studying processes at the level of individuals was argued to provide the best possibilities to embed the study of population dynamics in the theory of natural selection. In applying the ideal-free-distribution model to describe the distribu-

tion of foraging waders, interference-based approaches to population dynamics indeed adopt evolutionary thinking. The ideal-free-distribution model assumes that foraging individuals choose patches such as to maximise their intake rate. this assumption may be best justified through an argument of optimality, namely that natural selection can be expected to have weeded out all individuals that did not behave so as to maximise their intake rate. However, evolutionary considerations remain implicit; no account is made of the dynamics of evolution, nor is the performance of different patch choice strategies evaluated.

Studying processes at the level of individuals was also argued to have the intrinsic advantage that the properties of individual organisms and the mechanisms by which they interact with their environment are measured relatively easily, because of the temporal and spatial scale at which they operate (e.g., Huston et al., 1988). Although this argument depends on the species under study, it seems to apply to interference-based approaches to wader population dynamics.

Additionally, it was argued that individuals are the most suitable organizational units because they usually come in discrete entities, unlike units of other levels of organization (e.g., Łomnicki, 1992; Durrett & Levin, 1994). This argument would have applied to interference-based approaches to the study of population dynamics if these approaches would have been free of any considerations regarding populations. Such, however, is not the case; models are still phrased in terms of characteristics of populations (density), so they still rely on the fuzzy concept 'population'.

LINKING COMPETITION AND POPULATION DYNAMICS; WHY NOT (YET)?

Even though the link between interference competition and the dynamics of populations is a very interesting one, I have not touched upon it in this thesis. Quite deliberately, I have restricted my work to the study of the interference process in itself. Linking these processes to the dynamics of populations seemed (and seems) premature to me, given that understanding of the interference process still is rudimentary. In this section I discuss (1) why I think that it is studies of the interference process that are currently most wanted, (2) what my thesis has contributed and (3) the way to proceed in the study of interference competition and its consequences.

SUBTLE DIFFERENCE WITH STRONG EFFECTS

The decision to focus the work in this thesis on the interference process, rather than on its consequences in terms of population dynamics, or even in terms of the distribution of foraging animals over food patches, mainly stems from the

MECHANISTIC MODELS

The Beddington model

$$W = \frac{ax}{1 + at_h x + 2bt_f y}$$

The Ruxton model

$$W = \frac{ax}{1 + at_h x + \frac{2bt_f y}{1 + at_h x}}$$

Parameter interpretation

W	$\#s^{-1}$	intake rate
x	$\#m^{-2}$	food density
y	$\#m^{-2}$	forager density
a	m^2s^{-1}	area of discovery of food
b	m^2s^{-1}	area of discovery of competitors
t_h	s	prey per capita handling time
t_f	s	per capita fighting time
m	–	interference coefficient
q	m^{-2}	interference area
r	$\#m^{-2}$	reference forager density

PHENOMENOLOGICAL MODELS

The Hassell-Varley model

$$W = \frac{a(y/r)^{-m} x}{1 + a(y/r)^{-m} t_h x}$$

The Doublelog model

$$W = \frac{ax}{1 + at_h x} (y/r)^{-m}$$

The Semilog model

$$W = \frac{ax}{1 + at_h x} (1 - m \log(y/r))$$

The untransformed model

$$W = \frac{ax}{1 + at_h x} (1 - qy)$$

Figure 7.3. The six models of the generalized functional response reviewed by van der Meer and Ens (1997).

work of van der Meer and Ens (1997). I have already introduced this paper in the Introduction, but I will now present it in more detail.

Van der Meer and Ens (1997) start their paper by showing how the ideal-free-distribution model of Fretwell and Lucas (1970) can be used to derive predictions on the aggregative response from models of the generalized functional response. In general terms, this comes down to using the ‘ideal-free’ prediction that intake rate will be the same at all occupied food patches. Next, van der Meer and Ens (1997) gathered six different models of the generalized functional response from literature on interference competition among foraging waders (Figure 7.3). Two of these models had been derived mechanistically, through an approach resembling reaction kinetics; the other four had been derived phenomenologically. Next, they showed, both analytically and by means of a numerical example, that application of the ideal-free-distribution model to each of the six models of the generalized functional response yielded qualitatively different predictions of the distribution of foraging waders over food patches (Figure 7.4B). While some of the models of the generalized functional response

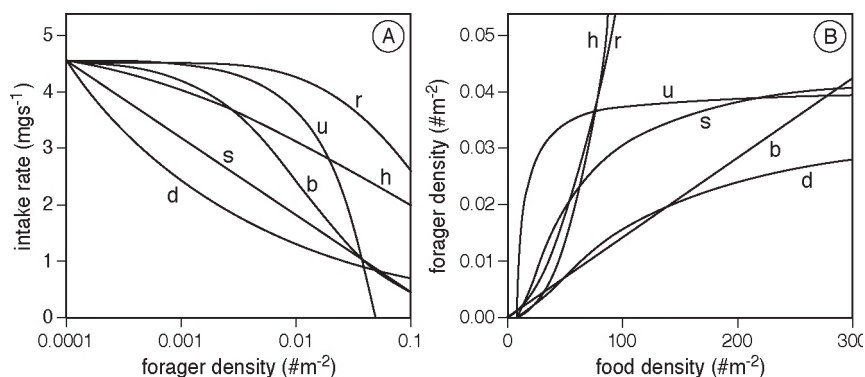


Figure 7.4. The relationship between forager density and intake rate as described by six models of the generalized functional response (A), and the predictions of the ideal-free-distribution model on the aggregative response, that is, the relationship between food density and forager density (B), for each of these six models. Model codes (h, r, b, d, s and u) and parameter values as in van der Meer and Ens (1997).

led to the prediction that forager density would be limited at high food densities (the Doublog, Semilog and Untransformed model), others led to the prediction that foragers choose patches in proportion to the food density at these patches (the Beddington model), or that foragers aggregate in the best food patches (the Ruxton model and the Hassell-Varley model). This result is striking especially because the six models yielded overlapping generalized functional response curves (Figure 7.4A) and because predictions on the aggregative response were all generated in the same way – by means of the ideal-free-distribution model.

What van der Meer and Ens (1997) showed is that predictions of the distribution of foraging waders over patches of food are sensitive to the precise form of the generalized functional response. Had the various models of the generalized functional response yielded more or less identical predictions of the aggregative response, it could have been argued that the details of the interference process did not matter. But such was not the case. Apparently subtle differences between models of the generalized functional response resulted in qualitatively different predictions regarding the aggregative response. This implies that the very choice of a model of the generalized functional response determines predictions of the aggregative response. This makes knowledge of the details of the interference process (the generalized functional response) an essential prerequisite for predictions of the aggregative response. It was this insight that was the motivation underlying my Ph.D. project to study the generalized functional response in more detail and to consider study of its consequence on the distribution of foraging animals and/or the dynamics of wader

populations premature. What sense does it make to study the consequences of an arbitrarily selected model of the generalized functional response, if these consequences are sensitive to the very choice of this model?

AN INCONSISTENT FRAMEWORK

Van der Meer and Ens (1997) provided one other argument that convinced me that understanding of the interference process was still wanting. Applied to foraging animals, the ideal-free-distribution model invokes the assumption that foraging animals behave so as to maximize their intake rate. This assumption is generally justified by the idea that such behaviour is the result of natural selection. No such assumption is made in the models of the generalized functional response reviewed by van der Meer and Ens (1997). These models treat foraging animals as 'aimless billiard balls' with no choice but to act aggressively when encountering each other. Whether or not such behaviour is adaptive is not considered. Thus, use of the ideal-free-distribution model in combination with models of the generalized functional response is not quite consistent.

THE NEED FOR MECHANISMS

Given that predictions of the aggregative response are sensitive to the generalized functional response model used to generate them, the obvious question is how to select among models of the generalized functional response. Van der Meer and Ens (1997) argue against the use of phenomenological models, because such models are 'both theoretically deficient and lacking empirical support'. They argue in favour of mechanistic models, because of the 'higher theoretic appeal' of such models. As mentioned above, mechanistic models are indeed generally thought to be intellectually more satisfying than their phenomenological counterparts, because they (can) provide an understanding of how phenomena come about, and because they can be extrapolated to novel conditions, or at least more so than phenomenological models. For the specific case of selection among models of the generalized functional response, a further important argument in favour of mechanistic models is that, because mechanistic models specify how the focal phenomenon comes about, they provide extra means to select among different models; mechanistic models can be selected on the basis of the assumptions regarding the mechanisms. This latter argument is particularly of relevance here, because the qualitatively different predictions of the aggregative response were generated from models that yielded overlapping generalized functional response curves (Figure 7.4A). The overlap in the generalized functional response curves implies that it will probably be very difficult, if not impossible, to select among models on the basis of any goodness of fit criterion. Data sets in ecology are generally so variable that selection of only subtly different models of the generalized functional response may not be possible. This argument seems supported by an as yet unpublished

analysis performed by Jeroen Minderman, who fitted the six models of the generalized functional response to the turnstone data of chapter 2. Indeed, in terms of explained variance, the fit was near identical for the various models even though parameter values sometimes differed considerably.

SOME MARGINAL NOTES

Are these reasons sound? I have come to realize that some marginal notes can be made. With regard to the reasoning that predictions of the aggregative response depend on the details of the generalized functional response, at least three objections can be made. Additionally, a marginal note can be made to the ‘inconsistent use of evolutionary thinking’ argument, to the ‘impossibility to select among phenomenological models of the generalized functional response’ argument, and to the very idea that two of the models reviewed by van der Meer and Ens (1997) would be mechanistic.

SUBTLE DIFFERENCE WITH STRONG EFFECTS

First, the methods used by van der Meer and Ens (1997) could be criticized for, in comparing the various models of the generalized functional response, van der Meer and Ens (1997) have used rather arbitrary parameter values. For each of the six models parameter values were chosen in such a way that the models generated overlapping generalized functional response curves. Such an approach seems hard to justify for it makes the comparison between models arbitrary. This point of criticism, however, may not be too important for the conclusions drawn from the analysis, because van der Meer and Ens (1997) also studied the behaviour of the generalized functional response models in qualitative terms, by comparing first and second order derivatives. This qualitative analysis ensures that their results will hold regardless of the specific parameter values chosen in the numerical analysis. To this it can be added that other ways of selecting parameter values are likely to lead to stronger differences in the predictions of the aggregative response, thereby strengthening the conclusion drawn by van der Meer and Ens (1997). In his analysis, Jeroen Minderman found that the six models, when fitted to one and the same data set, yielded generalized functional response curves with sometimes considerably different parameter values. As a result, differences in the predictions of the aggregative response became much more pronounced than those in the numerical example of van der Meer and Ens (1997). Thus, the more precise conclusions to be drawn from their study may be that the choice for a specific generalized functional response model qualitatively affects predictions on the aggregative response, *even when models generate overlapping generalized functional response curves*.

Second, on pragmatic grounds it could be argued that predictions of the aggregative response differ in part of the parameter space, and, thus, that the

relevance of the conclusion drawn by van der Meer and Ens (1997) depends on the food densities present and on the number of foragers in the system (van Gils & Piersma, 2004). Although this option cannot be excluded, it seems unlikely in the light of the point made in the previous paragraph that the analysis by van der Meer and Ens was conservative in that it was based on models that generated overlapping generalized functional response curves. The analysis by Jeroen Minderman suggests that when parameter values are selected by fitting the models to one and the same data set, there will not be any parameter range in which the predictions regarding the aggregative response overlap.

Third, it could be argued that the various generalized functional response models yield different predictions of the aggregative response, but that such differences need not to be reflected in changes in population size. At least in principle, it is still possible that the various models of the generalized functional response are irrelevant when these models are linked to models of the dynamics of populations. Whether or not this is the case remains to be studied. The preliminary study by Jeroen Minderman suggests that predictions of the mortality of foraging waders are sensitive to details of the generalized functional response models, but only quantitatively so.

THE INCONSISTENT USE OF EVOLUTIONARY THINKING

The argument that use of the ideal-free-distribution model in combination with models of the generalized functional response is not consistent because only the former assumes that foraging animals behave in an adaptive manner seems valid to me. Nevertheless, this argument should be treated with caution. Classification of a model being consistent with evolutionary thinking suffers from the same problem as classification of models as being mechanistic: it is a relative concept. Just as it is not possible to derive an entirely mechanistic model, it is not possible to study the evolutionary consistency of all elements of a model. To give an example: although the models presented in chapter 6 do consider the evolution of interference behaviour within the context of a Hawk-Dove game, they do not consider the adaptive value of either this game itself, or of the other model parameters, such as those capturing the foragers' searching behaviour and handling behaviour.

SELECTING AMONG PHENOMENOLOGICAL MODELS

It may be true that selection among phenomenological models of the generalized functional response on the basis of data on the relationship between intake rate and forager density is difficult. This argument, however, does not have to lead to the study of mechanistic models of the generalized functional response. Given that the various models generate different predictions, they may be selected on the basis of these predictions. In general it may be true that models either vary in at least one aspect, in which case it will be possible to select

among them, or they do not differ in any aspect, in which case selection among is not relevant. Against this pragmatic line of reasoning it can be argued that there is one drawback to selection among the phenomenological models on the basis of their predictions regarding the aggregative response; such requires the extra assumption that the ideal-free-distribution model (used to generate predictions) holds. Selection of phenomenological models on the basis of data on the generalized functional response would be independent of (ideas on) the distribution of foraging animals, whereas selection on the basis of the aggregative response is not.

INTERFERENCE PARAMETERS NOT YET INDEPENDENTLY MEASURABLE

The interference parameters of phenomenological models do not have a clear-cut mechanistic interpretation. They can only be found by fitting the models to data of the relationship between forager density and intake rate (searching efficiency). Interestingly, the same could be said for the two models assigned as 'mechanistic' by van der Meer and Ens (1997). These two models are very similar; they are both based on the reaction kinetic idea. They only differ in a detailed assumption on the foragers' interference behaviour: while the Ruxton model assumes that foragers in the searching state cannot interact with foragers in the handling state, the Beddington model assumes that they can. The two models contain the same two parameters related to interference competition: the 'area of discovery of competitors' and the 'fighting time'. Fighting time is generally interpreted as either a constant or as the average from an exponential distribution of fighting times, and should be independently measurable. Quantifying the area of discovery of competitors, however, is very difficult, if not impossible. The area of discovery of competitors generally has a 'mechanistic interpretation' as the area searched per unit time for competitors, but this search rate is hard to determine other than by fitting the models to data. This makes this parameter as much a 'mystery parameter' as the interference coefficient used in phenomenological models, at least according to the 'independently measurable' definition of the term mechanistic.

ARGUMENTS OF PRINCIPLE

These marginal notes notwithstanding, I still support the plea by van der Meer and Ens (1997) for studying the mechanisms of interference competition. By now, however, I prefer another argument for doing so. Van der Meer and Ens (1997) come to their plea through a practical argument, namely on the basis of differences in predictions of the aggregative response. The same conclusion can also be reached through an argument of principle. If it is a mechanistic understanding that is the goal of a research program, than mechanistic models are to be preferred regardless of their performance relative to phenomenological models, simply because phenomenological models do not yield a mechanistic under-

standing. This line of reasoning underlies the statement by Metz and de Roos (1992) that they prefer models based on mechanistic considerations over phenomenological models even if the latter provide a much better fit to data. In fact, this line of reasoning also underlies van der Meer and Ens' argument that use of the ideal-free-distribution model in combination with non-adaptive models of the generalized functional response is inconsistent.

Whether the argument of principle can justly be invoked, depends on the goal of the research project (Reflection I), as well as on the definitions used (Reflection II). If one strives to generate predictions, then predictive ability is the sole criterion for evaluation and it is the practical argument rather than the principle argument that should be used (see Reflection I). If the goal is to understand the distribution of foraging waders or the dynamics of their populations, then the principle argument may be preferred over the practical argument, though this depends on the definition of a mechanistic understanding. In mechanistic studies of the dynamics of populations, the use of phenomenological models of the generalized functional response is justified when either of the two hierarchical definitions of the term mechanistic (see Reflection II) is used, but not when the definition in terms of independently measurable parameters (see Reflection II) is used. In mechanistic studies of the distribution of foraging waders neither definition of the term mechanistic warrants the use of phenomenological models of the generalized functional response. This line of reasoning shows the importance of the specification of research goals.

Thus, by now, I consider the use of generalized functional response curves in mechanistic studies of the distribution of foraging waders and/or the dynamics of populations premature, because understanding of the interference process is still wanting. Models of interference competition account for only few of the mechanisms through which competition may arise, they have not yet led to an ability to generate *a priori*, accurate predictions, even the most mechanistic ones still contain parameters that cannot be measured independent of the model's structure, and attempts to study the evolution of interference parameters are but in their infancy (chapter 6).

WHAT DID THE PROJECT DELIVER?

Having explained why I have focused on the interference process itself rather than on its consequences, let me now address the question what this approach has yielded.

DETERMING THE GENERALIZED FUNCTIONAL RESPONSE

The experiments described in chapter 2 were among the first to study, at experimentally controlled forager densities, effects of forager density on the intake

rate of waders. Above all, these experiments convinced me of the limitations to understanding of interference competition. I found that forager density negatively affected the rate at which prey were discovered by both knots and turnstones. Nevertheless, only in turnstones did intake rate decrease with forager density. Knots compensated for the lower rate of prey discovery at higher forager densities by rejecting fewer prey. This conditional rejection of prey hints at the flexibility of behaviour and shows that social interactions may affect foraging success even in the absence of noticeable effects on intake rate. With regard to the mechanisms underlying the interference effects on prey-discovery rate, I found that knots and turnstones were affected in strikingly different ways. In knots, bird density had a complex, nonmonotonic effect on the time spent on vigilance and the time spent searching. In turnstones the main effect of increased bird density was a reduction in the prey-encounter rate, that is, the reward per unit search time. In neither of the two species did interference effects appear to result from an expected increase in time spent interacting. Other unexpected results of these experiments were that the allocation of time was independent of food density, that the dominance status of the focal turnstones did not explain variation in their intake rate, and that kleptoparasitic events were virtually absent in both experiments. Clearly, interference competition occurred for reasons other than those considered in models of interference competition, and the mechanistic basis of effects of forager density was more complex than generally assumed.

AN ALTERNATIVE INTERFERENCE MECHANISM

These findings left me puzzled with the question why knots and turnstones suffer from interference competition. Models of interference competition for food generally assume that interference arises from kleptoparasitism, that is, the stealing of food items. This mechanism can only be expected in systems in which the prey handling time is long (Brockman & Barnard, 1979). Such is usually the case for the bigger species. For many species, however, prey handling time may be so short that kleptoparasitism is not feasible. Knots and turnstones in the experiments described in chapter 2, for instance, swallowed their food very quickly, leaving little time for robbery. This implies that models of interference competition may as yet not be able to explain interference effects in perhaps the majority of cases. Why then do knots and turnstones suffer from interference competition? As the consumption of clumps of food may take time, even when the handling time of individual food items is short, I realized that interactions could potentially concern clumps of food rather than individual food items. This mechanism had been suggested several times before, but it had not gained firm ground in thinking on interference competition. As natural food distributions are often clumped, interactions over food clumps could be quite a general mechanisms of interference competition.

Chapter 3 starts with a review of experiments on the effect of the spatial clumping of food. Although not often considered in studies on interference competition, the idea that the spatial distribution of food can affect the behaviour of foraging animals had achieved ample attention in studies on resource defence. As I came to realise these studies of resource defence differ from studies of interference competition in that their main predictor variable is the distribution of food and not the density of foragers, and in that their main response variable is aggression and not intake rate. As a result, the two fields of study have developed in parallel but quite isolated. Few studies have actually considered the effects of both food distribution and forager density on both aggression and intake rate. The experiment described in chapter 3 does exactly this.

As it turned out, I found that the distribution of food was of prime importance for the extent to which focal turnstones suffered from interference competition. When food was dispersed, focal turnstones did not suffer from the presence of a competitor. When food was clumped, however, the presence of a competitor had a strong negative effect on intake rate, but only if this competitor was dominant over the focal forager. Apparently, dominant foragers could monopolize food but only when this was spatially clumped. This clearly supported the idea that interference effects could arise from interactions over clumps of food. The mechanisms underlying these effects, however, were not quite as we expected. Effects on intake rate were not reflected in the foragers' aggressive behaviour; dominant and subordinate foragers spent about the same amount of time interacting. Apparently, the monopolization of resource took only a few interactions. This, I attributed to the high familiarity among the turnstones. The lesson I drew from this finding was that it may be difficult to predict interference effects from the amount of agonistic behaviour observed; interference effects on intake rate may be unrelated to the amount of aggression. Again, I found that interference effects occurred for reasons other than those considered in models of interference competition.

DOMINANCE STATUS

The most striking result of the experiment described in chapter 3 was the very pronounced effect of the foragers' social dominance status. This effect was especially surprising because I did not find any effect of dominance in the previous turnstone experiment (chapter 2). The two experiments, however, differed strongly in the way I had treated the factor dominance. In chapter 2, I classified turnstones as 'dominant', 'intermediate' or 'subordinate' according to their absolute dominance position in a linear dominance hierarchy. In doing so, I assumed that foragers that have similar positions in a dominance hierarchy have more in common than foragers that take widely different position in the hierarchy. In chapter 3, on the contrary, I treated dominance as a relative characteristic; I made focal foragers 'dominant' or 'subordinate' by letting them forage in

the presence of a low-ranking or a high-ranking competitor, respectively. The rationale behind this approach is that foragers that are dominant over their competitor are comparable, even though they may take widely different positions in a dominance hierarchy. What my experiments revealed is that it is the latter approach that may be most appropriate. Apparently what matters for a forager is whether or not it is dominant over its competitor; not by how much it is so.

The importance of the forager's dominant status also made me realize the limitations of intake rate as a measure of fitness. Intake rate is the measure of performance generally used in studies of foraging animals. However, being a short-term response variable, it does not capture long-term processes such as the formation or maintenance of dominance relationships. Yet, such processes may be of prime importance for foraging animals, given that being dominant or subordinate may make all the difference. This implies that establishing dominance relationship may be one of the reasons why foraging animals interact with each other, or at least an important side-effect of agonistic interactions. Accounting for this insight would require a drastic change in the way we model the interference process for it would require considerations of both the short-term and the long-term consequences of interference behaviour.

FREE-LIVING TURNSTONES

The experiment described in chapter 4 concerns the question whether food distribution also affects the aggressive behaviour, intake rate and distribution of free-living turnstones. I found that the distribution of food did affect the wild foragers; when food was spaced out, the foragers were present in higher numbers, they interacted less frequently with each other, but they nevertheless spent about the same time on digging for food, my measure of their intake rate. These results support the finding of chapter 3 that the distribution of food may affect the foraging waders.

The main insight I gained from this experiment, however, is that experiments on free-living foragers differ in an essential way from experiments on captive foragers, so that direct, quantitative comparison between the two types of experiments is not straightforward. The crucial difference is in the treatment of the factor 'forager density'. In the laboratory experiment (chapter 3), I had experimentally controlled the density of foragers; this I did by forcing turnstones to forage on a specific foraging platform. As a consequence I could determine interference effects in the absence of feedback effects through patch choice. In the field experiment (chapter 4), forager density was out of my control; forager density was an uncontrolled response variable. Because free-living foragers can adjust their distribution over food patches, and hence their presence on my experimental plot, in response to, or even in anticipation of interference effects, feedbacks effects through patch choice were present in this experiment. The absence of feedback effects in the laboratory experiment and the

presence of such effects in the field experiment means that the two experiments address quite different questions. While the laboratory experiment addressed causal interference effects (the underlying process, so to say), the field experiment addressed observable patterns (the outcome of the interference process).

This insight had a strong effect on the way I analysed my field experiment. Clearly, the statistical design should do justice to the fact that forager density was an uncontrolled response variable and not an experimentally controlled predictor variable. Treating forager density as a response variable, however, implied the use of multivariate statistics, because aggression and intake rate were also affected by my experimental treatment, and because these three response variables could freely affect each other. In reviewing previous field experiments on the effect of food distribution, I realize that these studies generally had not acknowledged the multivariate nature of their data.

THE DIVISIBILITY OF FOOD

Chapter 5 presents another experiment at the intersection between the study of interference competition and the study of resource defence. By going through the publication process of chapter 3, I had come to realize the value of experiments that bridge these two fields of study. Initially, because of its meagre theoretical underpinning, I had not been much impressed by the literature on resource defence. It took me some time to realize that despite its weak theoretical foundation, the literature on resource defence was very valuable for its high number of experiments. This situation is almost the reverse of the situation in the literature on interference competition, where theory plays an important role, but where experiments are rare. Clearly, linking the two fields of study may be to the benefit of both. This motivated me to zoom in on the major differences between the two fields of study. One such difference concerns the way in which food is treated; while the studies of interference competition tend to think of food in terms of individual items, studies of resource defence usually consider food clumps.

In chapter 3 I discuss at some length whether it actually matters what foragers are fighting for; food items or food clumps. If food clumps do not differ from food items in a way essential to the interference process, it will be quite straightforward to adjust models of interference competition in such a way as to account for this alternative interference mechanism. If, on the contrary, the outcome of the interference process does depend on whether interactions are over food items or over food clumps, such requires further considerations. As one of the major differences between food items and food clumps I identified the extent to which they can be divided over multiple foragers, that is, their 'divisibility'. By definition, food clumps differ from food items in that they are composed of multiple items, and therefore their divisibility is higher. While some models acknowledge the potential importance of the divisibility of resources, few empirical stud-

ies have looked into this aspect, and these few studies did not consider its consequences for the interference process, which is the question that is addressed in chapter 5. In this chapter I anticipate that the divisibility of resources will become a crucial factor in future models of interference competition.

As it turns out, the extent to which foraging animals suffer from interference competition does depend on the divisibility of food. In the experiment described in chapter 5, I had manipulated this factor, along with the distance between food clumps and the foragers' dominance status. What I found was that subordinate foragers were able to get a share of the food only when food pits (the experimental devices containing food) were spaced out and when food within pits was divisible. These findings imply that to understand and predict interference competition the detailed characteristics of resources matter, and thus that in linking ideas from literature on resource defence with ideas from literature on interference competition differences in the divisibility of resources may be of special importance. Furthermore, the results of this experiment provided a strong corroboration of the findings of chapter 3, especially with regard to the striking importance of the foragers' relative dominance status. Again, the differences in the success of dominant and subordinate foragers were large and very consistent.

EVOLUTIONARY CONSISTENT

One motivation to focus my work on the generalized functional response was the inconsistency of use of the ideal-free-distribution theory in combination with models of the generalized functional response. The ideal-free-distribution model applied to foraging animals assumes that foraging animals behave so as to maximize their intake rate, and thereby use of the model invokes the idea that animals behave in an adaptive manner. No such considerations were made in the original models of the generalized functional response (van der Meer and Ens, 1997). In the course of my Ph.D. project, several interference models have been published that do consider the evolution of aggressive behaviour. Although these models seem to be very similar, they yield strikingly different predictions regarding the evolutionary stability of various interference strategies. In chapter 6 I compare some of the models of the evolution of interference behaviour. Although these models broadly have the same structure, they differ substantially in their detailed assumptions regarding, among other things, the structure of interactions, the presence of asymmetries and the payoff function. Although these differences may seem of minor importance, they turn out to strongly affect model predictions.

To unify previous approaches, chapter 6 contains a framework that allows for a more systematic approach to the study of the evolution of interference behaviour. I applied this framework to the previous interference models. By doing so, I have come to realize that modelling the evolution of interference behaviour

may not be such a straightforward task as it may have appeared at first sight. I found that many important aspects of the foraging game were easily overlooked, and that several important assumptions were not made explicit. Not only were the assumptions made by the various models not consistent with each other, several of the models also were internally inconsistent. That let me to plea for a more systematic approach and for the use of analyzing techniques that are more sophisticated than those generally used by evolutionary models of interference competition.

These suggestions may improve the way the evolution of interference competition is modelled and as such they may change ideas on the evolution of interference strategies. Indeed, preliminary analysis of a model that avoided some of the inconsistencies of previous models, already led to hitherto unpredicted outcomes of the evolution of interference behaviour. What I really learned from this chapter, however, has to do with the limitations of current understanding of the evolution of interference behaviour. Models of the evolution of interference behaviour are still utterly unrealistic with regard to several aspects, including variability of interference behaviour, dynamics of both food and forager density, variation in environmental conditions and differences between individuals, to mention but some. Among these aspects may well be the essence of the interference process. Furthermore, I have come to realize the intrinsic difficulty of linking models of the evolutions of interference behaviour to experiments. The evolutionary process operates at a time scale that cannot be studied experimentally, at least not in studies of foraging waders.

HOW TO PROCEED?

I started the work presented in this thesis with the conviction that understanding of interference competition is so wanting that use of models of interference competition in studies on the consequences of interference competition for the distribution of foraging animals and/or the dynamics of populations would be premature. This motivated me to focus on the competition process itself. As I have argued in the previous section, I think that this thesis presents some contributions to an understanding of the interference process. Above all, however, my work has strengthened my conviction that understanding of the interference process is still rudimentary. Therefore, I would argue that the next step in studying interference competition and its consequences should still concern the generalized functional response. I will now present some suggestions for future work.

SEPARATING INTERFERENCE FROM PATCH CHOICE

The one thing I have come to acknowledge is the difference it makes whether foragers are forced to forage on a specific patch or whether they are able to

choose between patches. Being clear about the status of observations on foragers in the absence or presence of patch choice may well help to clarify the study of interference competition. It is in the absence of patch choice that interference competition can best be determined. Observations on foragers that are free to choose between patches provide data on the outcome of the combination of the interference process and the distribution process. To study the basics of the distribution process, it may be equally desirable to initially exclude the interference process. This can be done by studying the patch choice of solitary foragers.

SPATIAL VARIATION AND SOCIAL DOMINANCE

What the experiments in this thesis suggest is that account of the small scale distribution of food and of the foragers' dominance status is an absolute must for models of interference competition among foraging waders.

Heterogeneity in the spatial distribution of food can in principle be included in models of the generalized functional response through statistical distribution functions. Such an approach would, however, be unwanted as it is not understood how such distribution functions come about. Perhaps a more fruitful way to account for heterogeneity in both the distribution of food and the within-patch distribution of foragers is by changing the way foraging behaviour is modelled. The generalized functional response is generally modelled through mean field equations; they are formulated in terms of (mean) food density and forager density. Alternatively, models of foraging animals could start from the movement rules of individual foragers, an approach generally referred to as Lagrangian. Of course, such models have already been developed (e.g., Turchin, 1998), but not often in the context of the social foraging; specifying social movement rules is difficult. The main advantage of such an approach would be that the distribution of food and foragers no longer has to be imposed; rather it follows naturally from the movement rules.

The importance of social dominance has, of course, been emphasized often before, and several models of the generalized functional response for unequal competitors have already been presented (e.g., Sutherland & Parker, 1985; Parker & Sutherland, 1986). The main difficulty in accounting for variation in social dominance position, however, is that it is difficult to do so in a non *ad hoc* fashion. Ideally, account of variation in social dominance status is based on ideas regarding the formation and maintenance of dominance hierarchies. The way to approach this question empirically would be to study groups of unfamiliar individuals. Previously, variation in dominance status has been accounted for by assuming that individuals come in discrete classes, being either dominant or subordinate. What my experiments suggest, however, is that any individual (except the most subordinate one and the most dominant one) is both dominant and subordinate; dominance status depends entirely on the status of the opponent. What varies between individuals is the frequency with which they are

in either position. This frequency will follow a uniform distribution. Once variation in dominance status is accounted for it remains to be determined how dominance relates to food intake. As my experiments show, this may well depend on environmental conditions such as the distribution and the divisibility of food.

DISTRIBUTION OVER FOOD PATCHES

Once the desired understanding of the interference process has been reached, it can be considered how interference competition affects the distribution of foraging waders. For this step, I would argue that much the same principles apply as I have been propagating for the generalized functional response. I think it will pay to develop a model that is both mechanistic and evolutionary. The ideal-free-distribution model is neither. It is not mechanistic, as it does not specify how animals choose patches (i.e., how animals gather information, how

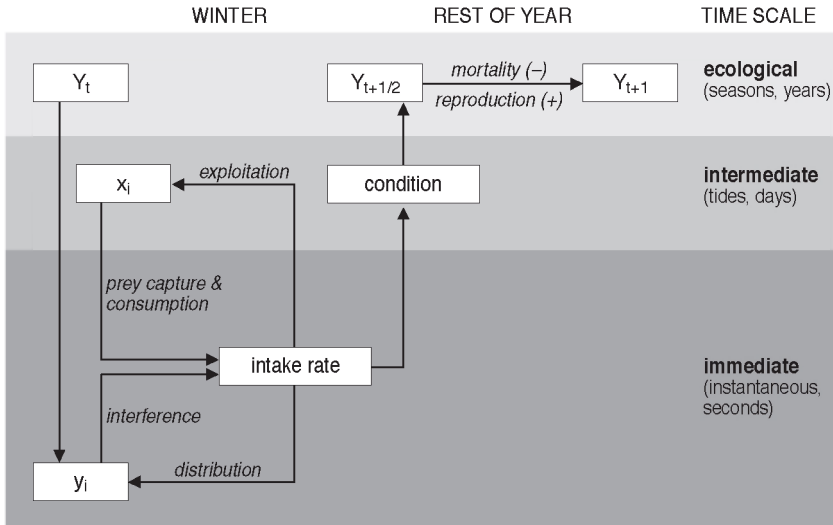


Figure 7.5. A process-rate-based framework to link the foraging behaviour of wintering waders to the dynamics of their population. The essential notion underlying this framework is that various processes operate at different time scales and that they can be separated accordingly. The density of predators (foragers) y_i at food patch i is assumed to change at a faster rate than the density of prey (food) x_i at this patch and than the condition (body mass) of the predators, which in turn are assumed to change at a faster rate than the population density of predators Y at the start of winter Y_t (the subscript j indicates a moment in the annual cycle), $Y_{t+1/2}$ the population density at the end of the winter and Y_{t+1} the population density at the start of the next winter). At the shortest time scale, the main assumption is that intake rate depends on the densities of prey (food) and predators (foragers) at specific food patches. At the longest time scale, it is assumed that the annual cycle contains two, distinct phases – ‘winter’ and ‘rest of the year’ – that are linked to each other only through effects on population density.

they move between patches). It is not evolutionary in that it studies neither the performance of different path choice strategies, nor the evolutionary dynamics of patch choice strategies.

LINKING INTERFERENCE TO POPULATION DYNAMICS

In developing interference-based approaches to population dynamics, I think much can be gained from exploring the linkages between hierarchical levels more systematically. To this end, the process rate based approach of O'Neill et al. (1986) may come in handy. Although hierarchies are generally defined in terms of levels of organization and not in terms of process rates, I think the latter way of looking at interference-based approaches of population dynamics might be illuminating: the dynamics of populations can be seen as the (slow) focal phenomenon and the behaviour of individuals as the underlying, fast process that is invoked to explain the dynamics of populations.

To illustrate this idea, I have slightly modified the frameworks presented in Figure 7.2 to explicitly arrange the various processes according to the time scale at which they operate (Figure 7.5). Specifically, I have assumed that the foraging process, including interference competition and the distribution of foraging animals, operates at a short, 'immediate' time scale, that is, that foraging is a fast process. In line with the definition of standing stock systems as 'systems in which food density changes at a time scale longer than that at which animals forage', I have assumed that the exploitation of resources operates at a somewhat longer, 'intermediate' time scale, being a slower process. Changes in the large scale population density are assumed to operate at an even longer, 'ecological' time scale. Looking at it this way, the essential notion underlying behaviour-based approaches to modelling the dynamics of populations thus is that processes operate at different time scales and that these time scales can be separated (in accordance with O'Neill et al. 1986).

Using this approach based on process rates, it immediately becomes clear that the real challenge for interference-based studies of population dynamics is the linkage between processes at the immediate time scale and processes at the ecological time scale. This can be done by aggregating the interference process in summarizing statistical properties that are preferably derived from the interference process itself (O'Neill et al., 1986; Flierl et al., 1999).

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REFLECTION I – A CRITIQUE FOR ‘A CRITIQUE FOR ECOLOGY’

Ecology is in crisis. There is a lack of scientific rigour, predictive capability is weak, and ecologists fail to harness modern technology. Indications of the poor condition of ecology include, among others, the lack of testable theory, low research budgets, lack of employment opportunities, and the proliferation of uncontrolled, uncoordinated studies. Most of all, however, the weakness of ecology as a science is revealed by our inability to solve ecological problems. While public demand and the practical necessity for attractive, powerful, ecological theory has mushroomed, the science has languished.

The above is the starting point of ‘A Critique for Ecology’ by Peters (1991), a thought-provoking book that criticises many an aspect of contemporary ecology. In essence, the book expresses the concern that ecologists have got their goals wrong. According to Peters, scientific theories must make testable predictions, so that ecology should be the branch of science that ‘seeks to predict the abundance, distributions and other characteristics of organisms in nature’. Peters’ major concern is that this is not quite what most ecologists do. Much of, especially academic, ecology is devoted to ‘understanding’ ecological observations. Understanding seems to have become a goal in itself; many studies do not even intend to make predictions. But, how to know whether something is understood if this cannot be tested? In the absence of predictive power claims of understanding cannot be evaluated independently. This analysis leads Peters to a plea for a ‘predictive ecology’, in which the focus is on the actual goal of science – making predictions. In principle, there are two kinds of theories that generate predictions and that can thus be used in predictive ecology. Empirical theories, such as statistical models, describe regularities in the world around us and predict likely patterns; explanatory theories predict and that tell why a system behaves as it does and therefore why predictions are valid. According to Peters the key tools of predictive ecology, however, should be empirical theories rather than explanatory theories. Opting for explanatory theories would ‘demand too much, too soon’. For now, ‘we should develop simple predictive tools that allow us to propose and confirm patterns that are relevant to the biological world. In future, such patterns may lead to more ambitious theory, but at present, they can serve as tool for environmental management, arguably a more pressing and important problem than creating a general field theory for ecology.’ For this reason, predictive ecology seeks patterns rather than explains them.

WHAT IF PETERS WERE RIGHT?

If the goal of science were to make predictions, making ecology a predictive science by focussing on empirical theory rather than on explanatory theory might not be such a bad idea. Simply because empirical theory has the sole purpose to

predict, whereas explanatory theory also wants to explain, empirical theories can in general be expected to outperform explanatory theories. This expectation is supported by Poole (1978), who states that to make predictions ‘statistical models are generally faster, cheaper, simpler and better predictors than their explanatory counterparts that attempt to predict and explain’. Poole bases this statement on experience in economics, where statistical prediction is used extensively. Peters also cites Cartwright (1983), for stating that in physics explanations are provided by general (explanatory) theories, but applied decisions are made with empirically justified calculating tools (empirical theory). Whether or not the same holds true for ecology, however, remains to be seen¹. Currently, the ability of ecologists to predict the course of everyday events is small regardless of the kind of theories invoked (of course, Peters would argue that this is because ecologists have been addressing the wrong kind of questions, focusing too much on understanding and too little on prediction, and not because ecology is fundamentally different from economics and physics).

There is one common argument against the view that statistical models provide the most efficient means to generate predictions. Statistical models are but interpolations; they have to assume that the future will resemble the past, and therefore they only work if the system is not changed dramatically (O'Neill et al., 1986; Peters, 1991). Often it is claimed that explanatory theory is less sensitive to such changes, because it is based on the processes underlying studied phenomena, and because processes are thought to change less than statistical relationships. Although this argument is appealing, it remains to be seen how often this argument applies; with certain changes explanatory models probably cannot cope any better than empirical models². Furthermore, it should be realized that what constitutes a change in a system depends on the domain of applicability of the statistical model. If the model is fitted on a dataset in which similar changes feature frequently, changes should not form a problem to the model.

WHY ISN'T PETERS RIGHT?

Although many of the concerns raised by Peters should be taken seriously, one might argue about his basic premise that the goal of science is to make predictions. At some point in his book, Peters himself states that ‘science lies at the interface between the abstract constructions of our mind and the phenomena of the external world’. Indeed, the general notion (Pickett et al., 1994 and references therein) is that science is about linking ideas (abstract constructs, theories) to observations (empirical stuff, data). This implies that the goal of science is to understanding nature (remember that understanding was defined as ‘the match between confirmable natural phenomena and independent predictions derived from conceptual considerations’; chapter 1), not just to predict it. Peters is right in saying that predictive ability is a necessary means to evaluate such understanding; this does not make predictive ability the ultimate goal of science.

WHERE DOES HE GO WRONG?

Peters bases his conviction that science is about making predictions on the ideas that 1) predictive power is what distinguishes science from nonscience and 2) that the goal of science should be formulated in terms of its distinctive characteristics. Let's have a closer look at these ideas. The first is about the demarcation of science. The statement cannot be true, for it implies that anything that has predictive power is science. Peters demarcates science on the basis of its performance, whereas science should be demarcated on the basis of its methods. If that is done, it is obvious that the second idea is equally problematic; the goal of science should not be formulated in terms of its methods. Thus, Peters' statement that science is about making predictions does not have a robust, rational foundation. Rather, I think, it stems from his desire to conserve nature and his conviction that the best way to do so is through predictive ecology³.

THE COROLLARY

Acknowledging that science is about understanding nature, it is obvious that predictive ability is not the goal of science. But, it could be argued, predictive ability may still be the ideal criterion to evaluate explanatory theories. After all, the proof of the pudding is in the eating, isn't it? Promising as this may look, there are several obstacles. It may be obvious that a match between theoretical predictions and observations does not guarantee understanding (to see this, just remember that statistical models may be very good predictors, even though they do not yield understanding). But there are other reasons why the evaluation of explanatory theories cannot be reduced to tests of their predictive ability. Let me present three of them.

LIMITATIONS TO DATA

First, data are not perfect. We all know that the collection of data is an ongoing process. The data we have today may be the best we can get, but there is no guarantee that it is a good description of nature or that we cannot improve it. More philosophically, the imperfection of data follows from the notion that objective data do not exist (e.g., Ford, 2000). All perceptions involve the brain, and as a consequence all observations depend in part on past experience, knowledge and expectations (Polanyi, 1969; Chalmers, 1982). As Fagerström (1987) puts it, 'rather than reporting what we see we report what we think that we see and this is what is possible to see and what is acceptable to see'. But even if all people could perceive signals in an identical way, observations would still not be objective, as all statements about observations are preceded by theory (observations are 'theory-laden'); what we observe and regard as meaningful depends upon theoretical preconceptions obtained before the activity of observation was begun (Chalmers, 1982; Fagerström, 1987; Haila, 1988). To give an example: measures of the dynamics of populations require a presupposition

about what is a population. The corollary of the notion that perfect data do not exist is that a mismatch between theory and data may be due to imperfect theory, but also to imperfect data.

PREDICTIONS TESTING DOES JUSTICE TO NEITHER THEORY NOR DATA

Second, theory has an internal structure. Each specific theory consists of several components (Pickett et al., 1994; Ford, 2000), such as facts, concepts, their mutual relationship and their domain of applicability. If a theory does not match a set of observations, it may be that only one of its components needs to be improved (Ford, 2000). Acknowledging this can help to design tests that do more than merely falsify a theory (Loehle, 1988)⁴. To this it can be added that there is an empirical and a logical component to the output of theories (Quine, 1981). Prediction testing involves evaluation of only the empirical output of a theory (its predictions). However, theories can do more than predicting data; theories may help to clarify matters (Levin 1980, 1981; Peters 1991), they may indicate what is possible (Levin, 1980, 1981; Peters, 1991; Odenbaugh, 2005), they may create intuition which may be used as a baseline against which to evaluate observations (Odenbaugh, 2005) and they may provide us with a conceptual framework through which we can conduct experiments and fieldwork (Levin, 1981; Odenbaugh, 2005). These issues are examples of the logical output of theory. It is important to realize that any theory can be evaluated on the value of either its logical output or its empirical output (or both). Note that this implies that even a theory that has limited predictive ability can still be very valuable.

Just as reducing theory to prediction generation does no do justice to the scientific process, it would be short-sighted to consider the evaluation of theories as the only value of data (Haila, 1988). Not all data are suited for that (Loehle, 1987); what, when and where questions, for instance, do not lend themselves easily for falsification. More importantly, not all data need to be used in tests either. Data can also form the basis of existential statements, pattern identification, analytical descriptions, and comparisons (Haila, 1988). An example of this statement is provided by the empirical chapters of this thesis.

THEORIES MATURE

Third, the formation of theory is a process. Theories often start out vague and qualitative. As more work is done on a theory, it matures. This as important implications for the idea of theory testing, because it implies that theories can be tested too early, potentially resulting in the premature rejection of a correct, but incomplete theory (Loehle, 1987). Pickett et al. (1994) identify three axes on which the maturity of theories can be evaluated. Mature theories are complete (domain, assumptions, concepts, definitions, facts, laws, models translation modes, frameworks), have well-developed individual components (exactitude, empirical certainty, applicability, derivativeness) and have well-integrated

components. Because it is difficult to test immature theories, it may often be better to invest in increasing the maturity of theories than in trying to prove or disprove the immature theory (Loehle, 1987).

WHERE DOES THIS LEAVE US?

There is but one conclusion that follows from these three issues (the imperfection of data, the internal structure of theory, and the maturation of theories): predictive ability cannot be used as the sole criterion for theory evaluation. Other criteria can be equally important. Peters mentions the following: relevance, immediacy, operationality, accuracy, generality, precision and quantification (these could all be regarded as aspects of predictive ability), economy of effort, practicability, simplicity, consistency with existing views, inspirational or heuristic effect, and elegance. To these I would add internal consistency and especially the reasonability of assumptions (Murray, 1986; Haila, 1988). How are we to combine these different criteria? There may not be an objective way to do so; evaluating theories is an art, whether we like it or not.

NOTES

- ¹ An example of a biological study that systematically compares the performance of statistical and mechanistic models is provided by Ellner et al. (1998), who analyzed data on measles epidemics in five large cities from the time before vaccination became standard procedure (which began in the 1960s). Ellner and coworkers compared the performance of one mechanistic model (the 'SEIR' model, which is based on the idea that populations contain susceptible, exposed, infective and recovered individuals), two phenomenological models (one based on feed-forward neural networks, the other based on linear autoregression) and a hybrid, semimechanistic model (which combines the mechanistic SEIR model with a regression model). These four models were parameterized and/or fitted on the first half of the data series and applied to predict the second half. As it turned out, the semimechanistic model outperformed both the phenomenological models and the mechanistic model in terms of explained variance, and one of the phenomenological models outperformed the mechanistic model. Thus, this study suggests that it may be hybrid models that do best in terms of predictive ability. However, to draw general conclusions from this study is not straightforward because the conclusions of Ellner et al. (1) apply to the average performance of their models (for specific cases other conclusions could be drawn), (2) may have been highly specific to the models and the data used, and (3) do not account for the amount of time and energy invested in either of the models. Clearly, ecology would benefit from more such systematic 'snapshot comparisons' of the performances of different kinds of models; they provide a clear-cut improvement over verbal claims of superiority.
- ² This is, for instance, clear from the data of the development of the Svalbard barnacle goose population as provided by Pettifor et al. (2000). Using a stochastic matrix model (i.e., an empirical model), Pettifor and coworkers were well able to predict the growth of the Svalbard barnacle goose population over the first twenty years of observation. After that, however, observations started to deviate rapidly from their predictions. Pettifor et al. (2000) mention several explanations for this sudden deviation of observed and predicted population size. Among others, the geese had discovered new, successful breeding grounds. To me, this indicates that dealing with drastic changes may be as problematic for explanatory models as for empirical models.

- ³ To be just, let me note that it would also be difficult to defend the idea that science is about linking ideas to observations. The fact that many references claim so may provide an argument of majority or of authority; it does not provide a rationale. Personally, I think there simply is not one a priori specified goal to science. Because this implies that we cannot take the goal of science for granted, it may well pay to be more explicit about our personal motivations so as to avoid endless polemics and much confusion.
- ⁴ It is this point that motivated me to test the assumptions of models of interference competition rather than predictions of specific models; it just seemed inefficient to me to test predictions of models that had dubious, untested assumptions. Although it may seem equally problematic to test assumption as to test predictions, this is not the case. Testing assumptions only implies statistical inference; testing predictions also involves scientific inference. The difference between statistical and scientific inference is that the latter involves explanations, whether the former just concerns patterns (Loehle, 1987).

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REFLECTION II – MECHANISTIC VERSUS PHENOMENOLOGICAL

The distinction between mechanistic and phenomenological models has been a recurrent theme in my thinking on interference competition among foraging waders. This distinction is, for instance, of importance for the evaluation of models of the generalized functional response, but it is also of importance for the rationale behind interference-based studies of the dynamics of populations (chapter 7).

In principle, the distinction between mechanistic and phenomenological approaches is straightforward. Phenomenological models merely describe a focal phenomenon, whereas mechanistic models additionally specify how this phenomenon arises. To give an example, while phenomenological models of interference competition consist of an empirically derived relationship between forager density and intake rate, their mechanistic counterparts are based on conceptual considerations of how the negative effect of forager density on intake rate comes about. Let me be more specific. In four of the models reviewed by van der Meer & Ens (1997) the interference effect is caught by a parameter referred to as ‘the interference coefficient’ (Figure 7.3). This parameter does not have a clear-cut interpretation in terms of the processes leading to interference competition. Instead, it can be found by regression intake rate (or the area of food discovery) against forager density (whereby the models differ in whether they log-transform intake rate and/or forager density). Because these models do not specify how interference effects come about, they are phenomenological. The two other models reviewed by van der Meer & Ens (1997) do specify how interference effects come about. Specifically, they assume (1) that foraging animals can be in one of three mutually exclusive behavioral states (searching, handling and fighting), (2) that two foraging animals enter the fighting state whenever they encounter each other, (3) that foraging animals search the environment for competitors at a constant rate (‘the area of discovery of competitors’) and (4) that interference competition arises from the loss of time spent fighting. In these two models, interference effects are caught by the area of discovery of competitors and the duration of a fight, two parameters that do have a clear-cut interpretation.

A FIRST COMPLICATION AND ITS SOLUTION

A first complication in distinguishing mechanistic and phenomenological models arises from the fact that phenomenological models can sometimes be given a mechanistic interpretation. Let me give an example by means of the type II functional response, that is, the relationship between food density and intake rate in which intake rate levels off at high food densities. Holling (1959a) first derived this relationship phenomenologically (in accordance with Figure 7.6A)

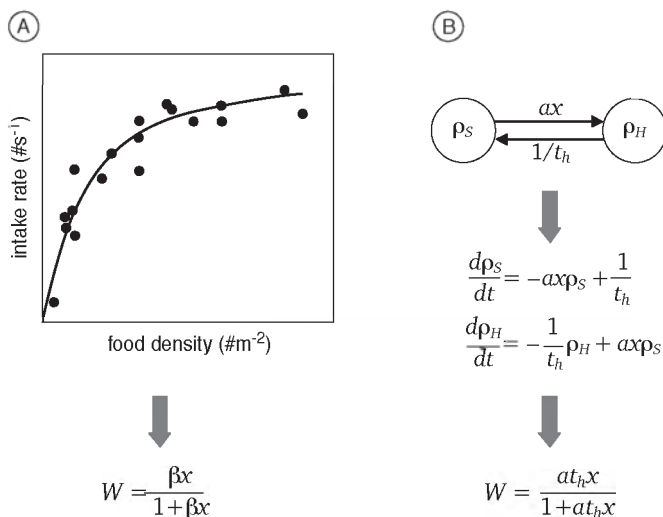


Figure 7.6. Schematic representation of a phenomenological (A) and a mechanistic (B) derivation of Holling's type II functional response, that is, his 'disc equation'. The phenomenological derivation starts from observations (black dots indicate hypothetical observations) on the relationship between food density x and intake rate W . The observed relationship can be caught analytically to provided a model of the functional response, where β is an unspecified coefficient. The mechanistic derivation starts from the idea that foraging animals are either searching or handling (ρ_S and ρ_H indicate the fraction of foragers in the searching state and in the handling state respectively). After specification of the transition rates (a is the area of discovery of food and t_h the per capita handling time of food items), a set of differential equations can be derived that keeps track of changes in the fraction of foragers in each of the two behavioural states. Assuming that equilibrium is reached, intake rate can be derived by solving the differential equations.

by studying the intake rate of a solitarily foraging deer mouse (*Peromyscus maniculatus*) in relation to experimentally manipulated densities of cocoons of the European pine sawfly (*Neodiprion sertifer*). In a subsequent publication (Holling, 1959b) he showed how this relationship could be derived mechanistically (in accordance with Figure 7.6B), from the assumptions (1) that solitary foraging animals can be in two mutually exclusive behavioural states (searching and handling), (2) that they search for food at a constant rate, and (3) that each food item takes a constant time to handle. This shows that the same equation can sometimes be derived both phenomenologically and mechanistically. Similar examples are provided by Kozłowski (1980), who showed that the logistic equation, which was originally derived phenomenologically, can be given a mechanistic interpretation, and by van der Meer (1997), who presented a mechanistic interpretation of the (phenomenological) Lotka-Volterra competition equations.

This complication can be solved rather easily. For that, we just have to remember that a model can be more than an equation; along with the equation may come a set of assumptions. This implies that the same *equation* may be derived in two different ways, but that the two derivations actually yield different *models*, because they involve a different set of assumptions. In terms of the previous example: derived from observations on foraging deer mice, the type II functional response forms part of a phenomenological model; derived from considerations on the behavioral states of foraging animals, the same equation forms part of a mechanistic model. Thus, while it may not be unambiguous to classify a certain equation as either mechanistic or phenomenological, classifying models as such should not be a problem.

A MORE SERIOUS COMPLICATION

A more serious complication arises from the relative nature of the term mechanistic. Defined as 'specifying how a phenomenon arises' the term mechanistic has an open end. Because this definition does not specify the level of detail required, any mechanistic model (but the one phrased in terms of nature's smallest particles) can be made more mechanistic by the addition of more detail. This implies that any mechanistic model contains phenomenological elements, that is, elements of which it is not specified how they come about. Let me make this clear by means of the mechanistic version of Holling's type II functional response model. This model predicts intake rate to level off at high food densities. To derive this prediction, the model assumes that animals search for food items at a constant rate and that each food item takes a constant time to handle. How these parameters come about, that is, for instance, why it takes a certain time to handle a food item, is not specified by the model. Yet, just as intake rate results from the searching and handling behaviour of foraging animals, these parameters result from certain processes (such as cognitive processes involved in searching and handling or physical processes involved in handling food items). In principle these parameters can therefore also be derived mechanistically. Because they are not, the mechanistic version of Holling's type II functional response is, to some extent, phenomenological.

Failing to acknowledge the relative nature of the term mechanistic is dangerous; it can lead to a practically endless spiral of reduction (Pickett et al. 1994; more whimsically, it can drag one into the 'swamp of reductionism'). Let me give an example of such a spiral. To study the dynamics of populations it can be argued that the underlying mechanisms, such as interference competition, should be studied to achieve a better understanding. While studying interference competition, however, it can subsequently be argued that the underlying mechanisms, such as the duration of fights, should be studied to achieve an even better understanding. What this example shows is that with an open definition of the term mechanistic, there is a high risk of mechanistic studies grow-

ing infinitely more mechanistic. The price that is paid for the increased level of detail is that with every level of extra mechanistic detail it gets increasingly difficult to focus on the focal phenomenon.

CLOSING THE TERM MECHANISM

The obvious solution to the danger of infinite regress is to make the term mechanistic absolute. Throughout my Ph.D. project I have considered three different ways to do so. The first two ways are based on the concept of hierarchies; the third way is based on ideas regarding the measurability of parameters. These three ways are not mutually exclusive; especially the third can easily be combined with either one of the two hierarchy-based definitions.

The general idea behind the two hierarchy-based definitions is the same: assuming that natural phenomena can be assigned to levels in a hierarchy, mechanistic studies can be defined as those studies that describe a phenomenon (operating at a certain level in the hierarchy) in terms of processes that operate on a lower hierarchical level (O'Neill et al. 1986). To avoid the swamp of reductionism, it can simply be specified that mechanistic models describe a phenomenon in terms of processes operating *at the one level below* that on which the focal phenomenon operates (Figure 7.7). The two hierarchy-based definitions differ in the way they distinguish hierarchical levels.

I	II	III	example
noise	noise	noise	...
noise	context	noise	communities
context	phenomenon	noise	populations
phenomenon	mechanisms	context	individuals
mechanisms	noise	phenomenon	organs
noise	noise	mechanisms	cells
noise	noise	noise	...

Figure 7.7. Illustration of the relative nature of the terms ‘phenomenon’ and ‘mechanism’ (modified from a lecture by Hannu Rita). Assuming that natural processes can be structured hierarchically, the hierarchical level below that of the focal phenomenon contains the mechanisms causing the phenomenon and the hierarchical level above that of the phenomenon forms its context; all other levels can be considered to be noise. Thus, processes at a certain level (in the example, the level of individuals) can be the focal phenomenon (I), the mechanisms of a higher-level phenomenon (II), or the context of a lower-level phenomenon (III).

THE LEVELS OF ORGANIZATION DEFINITION

In ecological literature, hierarchies are usually defined in terms of levels of organization (O'Neill et al. 1986). The classical hierarchy runs from molecules, through subcellular structures, cells, tissues, organs, organisms, populations, communities, and ecosystems to biospheres (Pickett et al., 1994), though various variations are around. In terms of levels of organization, mechanistic models describe phenomena at one organization level (say that of individuals) in terms of processes operating at the one level below (which would be the level of organs). Although the 'levels of organization' concept is very popular, it is not without difficulties. I will mention three of them.

First, identification of levels of organization may not always be unambiguous. The logistic equation, the Lotka-Volterra competition equations and the Lotka-Volterra predator-prey equations (Figure 7.1), for instance, are all generally considered to be population-level models. If population-level means 'containing characteristics that are specific to populations', the logistic equation and the Lotka-Volterra competition equations would indeed count as population-level models. The reason for this is that they contain a parameter K , the carrying capacity, that only has an interpretation as a population characteristic: carrying capacity can be interpreted as the maximum number of individuals that can be sustained in a system. Clearly, individuals do not have a carrying capacity. The growth parameter r of these models, however, can be interpreted either as the intrinsic rate of increase of a population, and hence as a population-level parameter, or as the average net contribution of individuals to the population size, which would make it an individual-level parameter. The way the growth parameter is interpreted does not change the status of the logistic equation or the Lotka-Volterra competition equations as population-level models, because there is only a population-level interpretation to the carrying capacity. However, the Lotka-Volterra predator-prey equations can be interpreted entirely in terms of individual-level characteristics, so that the status of this model as either population-level or individual-level is ambiguous¹.

Second, the classical levels-of-organization hierarchy (and many of its variations) is conceptually problematic, because it is a mixture of concepts of various types (Rowe, 1961). Ecosystems, for instance, have a physical structure, whereas populations and communities are abstract categories without such a structure. To avoid these conceptual problems, MacMahon et al. (1978) distinguish four different hierarchies. The classical levels-of-organization hierarchy is also conceptually problematic, because it assumes that lower level phenomena are nested within higher level phenomena. Allen and Hoekstra (1992) argue that such need not always be the case. Treating the human stomach as an ecosystem, for instance, ecosystems can be nested within individual organisms. To emphasize that levels of organization do not necessarily correlate with scale, Allen and Hoekstra (1992) propose a 'layer cake of ecology' model, in which they recognize the same

six levels of organization at each spatial scale. These attempts, however, have not yet succeeded to replace the popular, but problematic classical hierarchies.

Third, the levels of organization provide a means of structuring natural phenomena that is both rigid and coarse, and that may not always be operational. Consider, for instance, the negative effect of forager density on intake rate. If this is taken as the focal phenomenon, its mechanisms should be sought at the level of organs (classical hierarchy) or organ systems (MacMahon et al., 1978), assuming that this phenomenon lies at the level of organisms. Intuitively, this does not make much sense to me. Rather, I would look at the behaviour of individuals for a mechanistic understanding of such interference effects. But where does the behaviour of individuals fit in if natural processes are organized according to the levels of organization? Presumably, the behaviour of individuals should be assigned to the level of organisms, just as the negative effect of forager density on intake rate. According to O'Neill et al. (1986) this touches upon an essential problem of the levels-of-organization definition of a hierarchy. Forming a hierarchy on the basis of levels of organization may be intuitive, but it is neither operational, nor functional.

THE PROCESS-RATE DEFINITION

To solve the problems inherent to the levels-of-organization definition of hierarchies, O'Neill et al. (1986) make a strong plea for structuring natural phenomena on the basis of differences in process rates. According to O'Neill et al. each process in nature operates at a specific rate and a specific spatial scale. They give the following example: "... individual tree leaves respond rapidly to momentary changes in light intensity, CO₂ concentration, and the like. The growth of the tree responds more slowly and integrates these short-term changes. Change in the species composition of the forest occurs even more slowly, requiring decades or even centuries."² The variation in process rates and spatial scales allows for an arraying of processes in hierarchical levels, with processes corresponding to higher levels occurring at slower rates and at smaller spatial scales. The fact that variation in process rates occurs naturally gives the structuring of processes in terms of process rates the strong advantage (over, for instance, hierarchies based on levels of organization): the imposed structure is not arbitrary and can be derived empirically. A further advantage of defining hierarchical levels in terms of response times is that it naturally leads to the isolation of hierarchical levels. Generally, lower hierarchical levels communicate only their average responses to the higher levels; in this way each level acts like a filter. Again, O'Neill et al. provide an example of this in terms of trees. Fast changes in light availability affects photosynthesis, which operates at a low hierarchical level, but are not reflected in the annual growth response of trees; they are filtered out. Only the average (integrated) response is seen in the growth increment at the level of the tree.

How does this relate to definitions of the term mechanistic? If natural phenomena are assigned to hierarchical levels according to their process rates, mechanistic models can be defined as those models that explain slow processes in terms of faster processes. This sounded rather abstract to me, until I realized that an example of this could be found in interference-based approaches to the study of population dynamics. Essentially what is done when interference is invoked to study the dynamics of populations is to explain a slow phenomenon (population dynamics) in terms of a faster phenomenon (interference competition). I will not elaborate this insight here; it features in chapter 7 of this thesis.

Although I find the idea to define mechanistic in terms of a hierarchy based on process rates intriguing, this is not the definition that I have used throughout my thesis. In part this is because I encountered the idea only recently, but it is also because I am not yet convinced of its applicability. It remains to be seen whether processes in general operate at distinct time scales and whether these time scales can be identified objectively. Furthermore, I am not convinced that this way to define hierarchies provides a fruitful way to close the definition of the term mechanistic either. For that it should be possible to objectively determine which rate is the one operating below the rate of the process of interest; this may well be difficult.

THE INDEPENDENT MEASURABILITY DEFINITION

The third way to make the term mechanistic absolute is based on the definition of the term mechanistic as specifying how a certain phenomenon arises, but extends it by adding the condition that the parameters of mechanistic models should be measurable independently of the structure of the model in which they feature. This extra condition weeds out all models that contain what I refer to as ‘mystery parameters’, that is, parameters that do not have a clear-cut interpretation in terms of the processes through which the focal phenomenon comes about. Mystery parameters cannot be measured but through fitting the model in which they feature to observations on the focal phenomenon. Such is unwanted, because it implies that parameter values only have an interpretation in the context of the model in which they feature and because it requires the assumption that the model in which they feature is correct. Let me give an example. The logistic equation contains one mystery parameter – the carrying capacity. The way to quantify this parameter is to realize that the model predicts population growth to level off at the carrying capacity, to assume that the model is correct, and then to determine the asymptotic population size. Having to assume that the model is correct is very problematic as there are many reasons why the model would not be correct, in which case population growth would level off at a population size other than the carrying capacity. Furthermore, if model parameters cannot be estimated without assuming the model to be correct, there is no independent way to study the correctness of

the model. The use of mystery parameters precludes the independent evaluation of models.

Does the condition that model parameters should be independently measurable make the definition of the term mechanistic absolute? I think so, because it provides a clear endpoint to mechanistic studies. If the goal is to model a certain phenomenon mechanistically, this goal is achieved when the first model is developed in which all parameters are measurable independently of the structure of the model in which they feature.

NOTES

- ¹ This ambiguity can be avoided if the definition of a population-level model is changed from 'containing parameters that can only be understood in terms of population-level characteristics' to 'not accounting for between-individual variation'. The logistic equation, the Lotka-Volterra competition equations and the Lotka-Volterra predator-prey equations are all phrased in terms of the average individual; none of them accounts for variation between individuals, and therefore this new definition would ensure that they all have the same status as population-level models.
- ² O'Neill et al. (1986) find a further example in the work by Sollins et al. (1983), who analyzed soil organic matter accumulation at mudflows on Mt. Shasta, California. Over centuries, major changes in organic matter result from fire-initiated secondary succession. On a finer time scale, that of years, net accumulation of organic matter is due to annual litter-fall and decomposition. At the even finer time scale, that of days, organic matter changes due to wind-blown additions and removals and to the action of large decomposer organisms.

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