Interference Competition and Animal Distribution:
An Approach Based on the Dynamic Energy Budget (DEB) model

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THEORETICAL FRAMEWORK

Interference competition

Interference has been defined as a (reversible) decline in intake rate due to the presence of competitors (Goss-Custard, 1980). Interference competition entails the effect of social interactions on an animal's intake rate and is regarded as one of the major factors that influence the distribution of foraging animals (e.g. Goss-Custard 1970; Van der Meer and Ens 1997; Parker and Sutherland 1986).

Interference competition among predators may arise from a variety of mechanisms including prey depletion (Goss-Custard 1980), kleptoparasitism (prey steeling, Brockmann and Barnard 1979), displacement from rich micro-sites (Dolman 1995) and prey depression ("anti-predator responses of the prey to the presence of the forager"; Goss-Custard, 1970). In prey depression, interference occurs because as foragers have searched more areas, the density of prey that can be both detected and caught decreases so that forager intake rates decrease (Yates *et al.* 2000). Furthermore, foragers may fight or delay searching for prey upon encountering a conspecific, which decreases their overall intake rate. In this case, time is wasted instantaneously although foragers may gain future benefit from reduced competition.

Interference competition and animal distribution

The distribution of foraging individuals can be summarised in patterns of patch rejection. Factors that determine patch rejection are food, predation, competitive ability, dominance and interference competition. My PhD-research focuses on effects of interference competition on the distribution of animals. Interference competition can even serve as a stepping stone between individual behaviour and population dynamics (Peckarksy *et al.* 1997; Visser *et al.* 1999), particularly when the observed decline in food intake rate is the consequence of behavioural responses of individual foragers to increased intraspecific competition.

Food intake rate can be modelled as a function of prey density by means of the Michaelis-Menten equation {73} (Kooijman 2000) and is referred to as the functional response. For more than one predator, food intake rate can be modelled as a function of both prey density and predator density and is referred to as the aggregative response. The aggregative response thus predicts the aggregation of animals depending on density of prey on different food patches, assuming that animals maximise their fitness by maximising their food intake rate. The ideal free distribution theory, IFD, (Fretwell & Lucas 1970) describes the distribution and aggregation of animals that are '*ideal'* and '*free'*. 'Ideal' meaning that they are assumed to be equal in competitive ability, omniscient, and to consistently go to the patch where their intake rate is highest, and 'free' in that they are able to enter any patch without restriction or costs. Additionally, animals are assumed to all be alike. If the functional response is known, then one can subsequently derive in what way 'ideal' and 'free' animals will distribute themselves between patches of different prey density at a single moment in time (Van der Meer & Ens 1997). Providing that individuals are identical, this means that intake rate is equal across patches, 'ideal' and 'free' animals will distribute themselves among patches such that no predator can increase its reward rate by moving to another patch. In the absence of interference predators will aggregate in the patch with highest prey density, where animals obtain the highest possible intake rate. Such strong aggregation is of course unlikely; in many cases predators will interfere with each other, so that intake rates decrease with increasing predator density. As a consequence some predators will move to areas with lower prey density since this will increase their intake rate. To model this situation interference must be incorporated in the (ideal free) distribution theory.

Interference competition models of animal distribution

Interference competition models model the distribution of 'ideal' and 'free' animals and can be divided in two groups with regard to the assumptions on the supply of resources in the system (Sutherland & Parker 1986; Van der Meer & Ens 1997). (1) Immediate consumption systems, where resources are assumed to arrive in a patch at a constant rate, and resource items are assumed to be eaten instantly after arrival. (2) Standing stock systems, where animals are assumed to forage in patches with a fixed resource density, i.e. a fixed standing stock, without time in the dimension (Lessells 1995). An ideal and free distribution so predicted only applies to a single moment in time. Immediate consumption models do not represent the most common type of natural foraging situation, e.g. when animals search patches for dispersed prey that can be assumed to remain at constant density in the short term. Standing stock systems resemble the natural processes of foraging much closer than immediate consumption models do. For this reason, this essay will concentrate only on standing stock systems.

Within standing stock system modelling, two approaches have been taken to model decreasing intake rates with increasing predator densities due to interference competition among predators. The first approach uses some empirical relationship between searching rate (Hassel & Varley 1969) or intake rate (Sutherland 1983; Sutherland & Parker 1986) and predator density to model the effect of interference. The second approach assumes that animals are in different (mutually exclusive) states (e.g. 'search', 'eat' and/or 'interfere') where transition rules between the states formulate a set of differential equations describing their dynamics (Ruxton *et al.* 1992). The two approaches are referred to as *phenomenological* and *mechanistic*. Since the phenomenological approach lacks any mechanistic understanding, the mechanistic approach is preferred.

Ruxton *et al.* (1992) examined a series of detailed mechanistic behavioural models of the predation process in a homogeneous environment. They adopted an approach borrowed from chemical reaction kinetics to calculate food uptake per unit time per predator (functional response). The predator population is divided in several mutually exclusive states. Given the transition rules between the states, the functional response follows from the steady-state solution of the accompanying differential equations (note that the mechanism through which interference occurs is time wasted in agonistic behaviour). For example, if a searching and a handling state are distinguished, each transition from handling back to searching is supposed to mean that a prey is eaten. An encounter between predators could mean that a (searching or handling) predator stopped its pursuits and entered the 'fighting' state.

Several workers (Stillman *et al.* 1997; Stillman *et al.* 2002) have used the approach of Ruxton *et al.* (1992) to predict strength of interference between foraging animals and tested model predictions using field observations of shorebirds feeding on a range of prey species. In short, the model (Stillman *et al.* 1997; Stillman *et al.* 2002) progresses in discrete time steps and follows the location and behaviour of each animal within a population as they encounter prey and competitors. Animals can be either searching for or handling prey, fighting over prey or avoiding competitors. They either find prey independently or steal prey from a competitor. Interference occurs when animals waste time avoiding and fighting, and when prey is stolen (note that in this case interference occurs through two mechanisms). The responses to competitors are calculated using intake rate-maximising decision rules. The model assumes a strict dominance hierarchy, so that the more dominant individual in a dispute always wins regardless of the absolute difference in dominance.

Van der Meer & Ens (1997) illustrate the problem that predictions on patch distribution of ('ideal' and 'free') predators strongly depend on the assumptions that are made on the effects of interference on intake rate. For example, their results, which only apply to a single moment in time, imply that it is of importance whether or not models take into account the fact that handling individuals may suffer from interference. The consequences in terms of the aggregative response are then serious: models that assume that handling individuals are not susceptible to interference (e.g. Hassell & Varley 1969; Ruxton *et al.* 1992) predict that proportionally more predators aggregate in high prey density patches. Models that are based on empirical relationships between intake rate and predator density (Sutherland & Koene 1982; Ens & Goss-Custard 1984; Goss-Custard & Durrell 1987) predict a limited predator density in the best patches (Fig. 1a, b). The study of interference competition therefore requires detailed behavioural observations to fully understand the mechanistic basis of competitive interactions and to give accurate predictions of effects of interference on the distribution of animals.

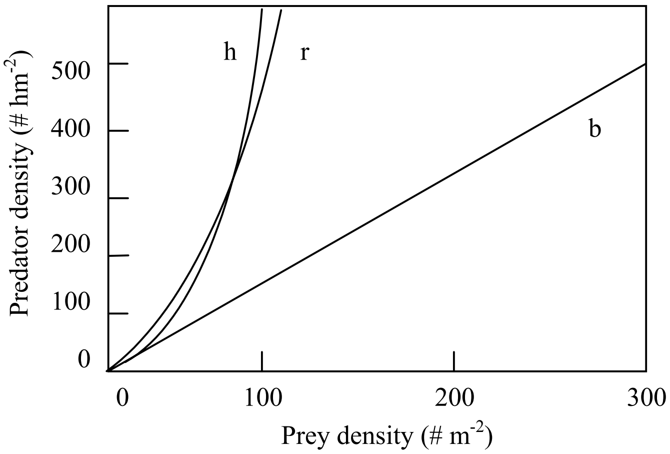

Fig. 1a. The aggregative response functions, i.e. the density of predators at which each predator can obtain an intake rate of $4{\cdot}10^{-3}$ # sec^{-1}. h Hassel & Varley (1969), b Beddington (1975), r Ruxton *et al.* (1992) (Van der Meer & Ens 1997).

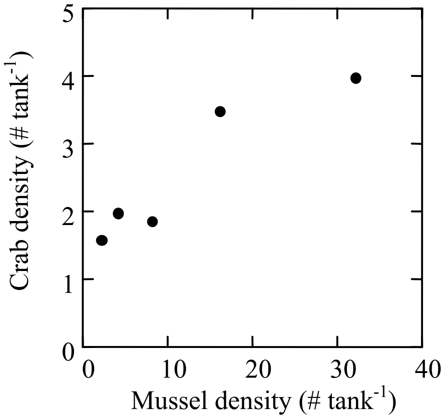

Fig. 1b. The aggregative response at which shore crabs (*Carcinus maenas*) can obtain an intake rate of 0.1-0.2 mussels (*Mytilus edulis*) min^{-1}. diameter of tank =56 cm

APPLICATION OF INTERFERENCE COMPETITION IN THE DEB MODEL

Competition in the DEB model

Competition among species in the DEB model occurs through the substrate that both species feed on. The interaction between individuals of the same species is restricted to feeding on the same resource as well. The argumentation {311} (Kooijman 2000) is that the general idea (at the population level) is to study the consequences of feeding on the same resource and not to produce population models that are as realistic as possible. However, as is evident from the above, interference competition affects the distribution of animals and thus indirectly affects competition for food resources and may ultimately affect the population dynamics of the species.

Interference competition and the aggregative response incorporated in the DEB model

In the DEB model animals are considered synthesising units {43} (Kooijman 2000) where food particles arrive and an animal 'handles' a food particle upon arrival for a certain period and searches for or 'binds' food particles in between the end of a handling period and the next arrival. In the DEB model these synthesising units only interact via (depletion of) food particles. In order to incorporate interference competition and the aggregative response, it is necessary that the synthesising units interact.

Interference competition could be incorporated in the DEB model via the functional response, described at {74} (Kooijman 2000) where

$$\dot{J}_X = \dot{J}_{Xm} \cdot X(\dot{J}_{Xm}/\dot{F} + X)^{-1}. \tag{1}$$

This functional response can also be derived in the following way (cf. Van der Meer & Ens 1997; Ruxton *et al.* 1992). Predators are assumed to be either in the (mutually exclusive) handling (H) or searching (S) state with transition rules

S→H: $\dot{F} \cdot X \cdot S$

H→S: $\dot{J}_{Xm} \cdot H$.

Hence, at equilibrium,

$$H = \dot{F} \cdot X \cdot S / \dot{J}_{Xm} \text{ and } S = S \text{ with } S + H = 1 = (1 + \dot{F} \cdot X / \dot{J}_{Xm}) \cdot S \text{, so } \dot{F} \cdot X \cdot S = \dot{F} \cdot X(1 + \dot{F} \cdot X / \dot{J}_{Xm})^{-1}.$$

The intake rate or functional response (cf. (1)) is then given by

$$\dot{J}_X = \dot{F} \cdot X \cdot S = \dot{J}_{Xm} \cdot \dot{F} \cdot X(\dot{J}_{Xm} + \dot{F} \cdot X)^{-1} = \dot{J}_{Xm} \cdot X(\dot{J}_{Xm}/\dot{F} + X)^{-1} \tag{2}$$

If predators interact and if, for instance, searching predators (P) interact with both searching and handling individuals, predators are either in the (mutually exclusive) handling, searching, or fighting (W) state with transition rules

S→H: $\dot{F} \cdot X \cdot S$

H→S: $\dot{J}_{Xm} \cdot H$

S→W: $\dot{F}' \cdot P \cdot S$

W→S: $\dot{J}'_{Xm} \cdot W$.

Hence, at equilibrium,

$$H = \dot{F} \cdot X \cdot S / \dot{J}_{Xm}, W = \dot{F}' \cdot P \cdot S / \dot{J}'_{Xm} \text{ and } S = S \text{ with } S + H + W = 1 = (1 + \dot{F} \cdot X / \dot{J}_{Xm} + \dot{F}' \cdot P / \dot{J}'_{Xm}) \cdot S \text{, so}$$

$$\dot{F} \cdot X \cdot S = \dot{F} \cdot X(1 + \dot{F} \cdot X / \dot{J}_{Xm} + \dot{F}' \cdot P / \dot{J}'_{Xm})^{-1}, \tag{3}$$

which is an approximation of Beddington's (1975) functional response (here $\dot{F}'$ represents the encounter rate with competing predators and $\dot{J}'_{Xm}{}^{-1}$ represents the average fighting period). The intake rate is also given by

$$\dot{J}_{X} = \dot{F} \cdot X \cdot S = \dot{J}_{Xm} \cdot \dot{F} \cdot X(\dot{J}_{Xm} + \dot{F} \cdot X + \dot{F}' \cdot P \cdot \dot{J}_{Xm} / \dot{J}'_{Xm})^{-1} = \dot{J}_{Xm} \cdot X(\dot{J}_{Xm} / F + X + \dot{F}' \cdot P \cdot \dot{J}_{Xm} / F \cdot \dot{J}'_{Xm})^{-1} \quad (4)$$

More complex models naturally exist where distinctions are made as to which predators and in what state fight with each other. Hitherto animals exhibit different competitive abilities and the spatial distribution of predators differing in competitive abilities is also rather sensitive to different mathematical formulations of phenomena observed at the individual level (Van der Meer 1997). Again this emphasises the importance of interference competition and its effect on the aggregative response of animals with its consequences at the population level.

PRACTICAL APPROACH OF THE STUDY OF INTERFERENCE COMPETITION AND ANIMAL DISTRIBUTION

The experimental study of the effects of interference competition on animal distribution requires thorough knowledge of the mechanisms through which interference competition occurs and of the influence of predator density and competitor size on the time budget of foraging animals. Furthermore an ideal and free prediction of the distribution of animals in a standing stock system only applies to a single moment in time; an experiment would then require immobile prey at a constant density during the course of the experiment, for instance shore crabs foraging on mussels present at a constant density (Fig. 2). To arrive at ideal free predictions however, validation and/or adjustment of the aggregative response (3) is the first step, followed by a measurement of the competitive weight of animals. Observed intake rates of animals of different competitive abilities (most often directly related to size of the animal) together give the probability of an animal obtaining a food item (Houston & McNamara 1988; Milinski 1988). With more than one food patch, a prediction of an ideal and free distribution involves matching the proportion of (competitive) abilities to the proportion of food available; such a distribution can be tested experimentally.

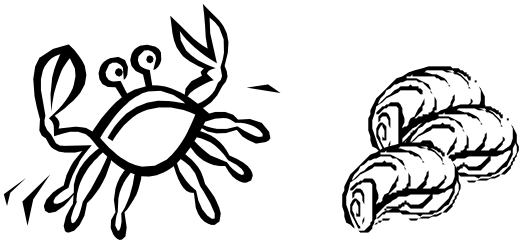

Fig. 2. An active predator (shore crab) foraging on inactive prey (blue mussels, *Mytilus edulis* L.).

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