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Model for integrating internal and external drivers for dispersal and distribution pattern in carabid beetles

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Abstract: Carabid beetles are important contributors to the ecosystem service of biological control of invertebrate crop pests. The density of carabid beetles varies over the landscape and their spatial pattern is highly dynamic in time and space. We hypothesize that the ever changing pattern of carabids in the landscape, and the spatial distribution of the associated ecosystem service, may be predicted by integrating internal and external drivers into a behavioural model for individuals. Internal drivers include the need for food, egg laying substrate and shelter. External drivers include the spatial pattern of food items, structure and density of vegetation, microclimate, and the presence of conspecifics or predators. Both types of drivers show strong seasonal variability. Process data will be collected in artificial arenas with automated camera observation of behaviour of *Pterostichus melanarius* and *Poecilus cupreus*. Here, the conceptual framework of the modelling is explained together with the experimental approach and some expected outcomes. One strong and one weak point of our approach are discussed.

Key words: Carabid beetles, population distribution, walking behaviour, internal- and external drivers of behaviour

Introduction

Dispersal processes play a key role in determining population distributions of animals in space. Within fields, beetles tend to aggregate into species specific patches that do not change a lot during summer, but which may differ between years (Holland et al., 2005; Thomas et al., 2001; 2006). Previous studies correlated environmental factors, such as plant density, vegetation type or soil moisture content with population densities to explain spatial patterns. Although these studies have provided much knowledge about environmental factors that correlate with population distributions, the mechanisms that drive dispersal are not well understood. To understand these mechanisms we need to know what beetles respond to and what they are motivated for. We assume that beetles respond to prey density, to suitability of the substrate for egg-laying, to shelter, to natural enemies and to conspecifics. The motivations, or the internal driving forces that we distinguish are need for food, need for egg-laying substrate and need for shelter. We hypothesize that changing distribution patterns of carabids in the landscape may be predicted by integrating these motivations with external driving forces of movement into a behavioural model for individuals. In this paper we explain the conceptual framework for this model, the experimental approach and some expected outcomes.

Conceptual framework

In our conceptual framework (see Figure 1) we distinguish between internal and external driving forces of carabid walking behaviour. Based on data from earlier research on carabids we assume the need for food, egg-laying substrate and shelter as major internal driving forces (or motivation states) of carabid walking behaviour. The need for food can be defined by satiation state and the need for egg-laying substrate by egg maturity. Mols (1993) and others (see Table 1) quantified in detail walking behaviour in relation to satiation state. Egg maturity has not been related to walking behaviour in literature, but because beetles do have a clear preference for certain egg-laying substrates (Tréfás & Van Lenteren, 2004), we hypothesize that females that have mature eggs will adapt their walking behaviour till a suitable egg-laying substrate is found. Satiation state and egg maturity have a strong interrelationship (Mols, 1993). Need for shelter plays a role at the end of the daily activity period and at the end of the season when beetles move to hibernation sites. How the need for shelter influences walking behaviour has not been studied yet. Satiation state, egg maturity and need for shelter are in this model assumed to be controlled by the circadian and annual cycle of beetles.

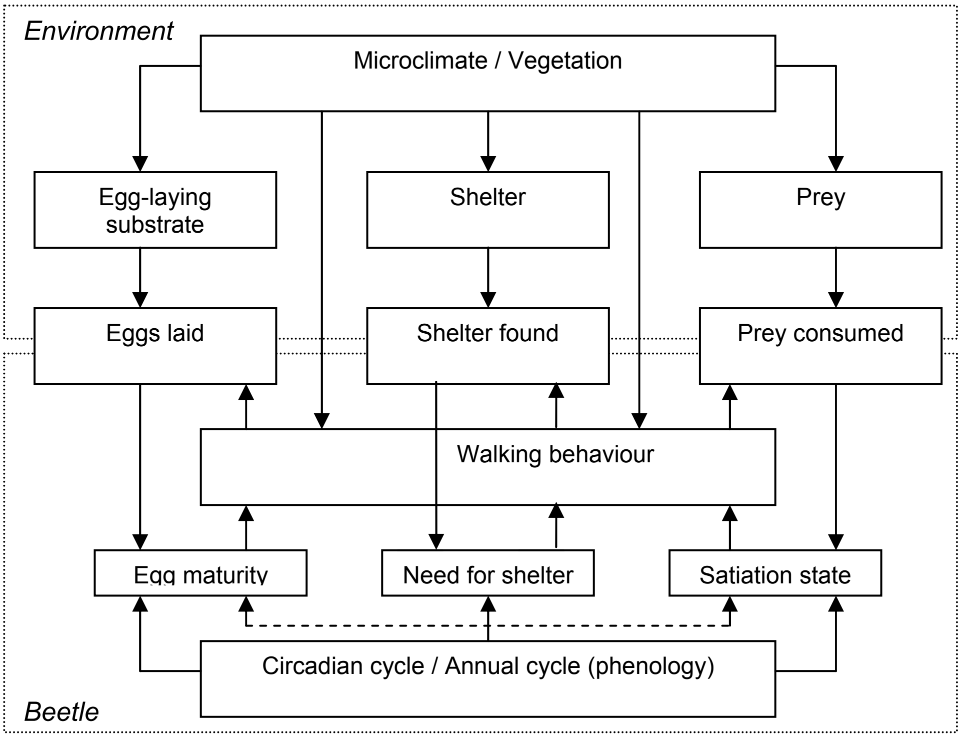

Figure 1. Relation diagram with external drivers of walking behaviour (top half of figure) and internal drivers (bottom half of figure).

We assume that the major external driving forces of walking behaviour are: availability of egg-laying substrate, prey availability and presence of shelter. The internal driving forces determine the beetles' motivation to show a particular walking behaviour, which is triggered and affected by external driving factors. The resulting behaviour determines whether a resource is found or not. In our model egg laying, prey consumption or finding a shelter has a feedback on walking behaviour through changes in motivation (egg maturity, satiation state or need for shelter) of the beetle. These feedback mechanisms are acting on the level of internal physiology of the beetle. This integration level is essential for the model but it is not addressed in our experiments. Availability of egg-laying substrate, shelter and prey density are all three determined by local microclimate and by the structure, density and species composition of the vegetation and beetle density (see table 1 for references). Also, vegetation may have a direct effect on walking behaviour by the resistance it causes for movement (Jopp & Reuter, 2005).

Table 1. Studies on some of the relationships that are shown in Figure 1.

Relation	Reference
Satiation state – Walking activity	Fournier & Loreau (2001) – Ecol Entom 26 Frampton et al. (1995) – Biological Conservation 71
Satiation state – Walking behaviour	Mols (1993) – PhD thesis, Wageningen University Wallin & Ekbom (1994) – Pop Ecology
Vegetation density – Walking activity	Tréfás et al. (2003) – IOBC wprs Bulletin 26
Microclimate – Walking activity	Tréfás et al. (2003) – IOBC wprs Bulletin 26 Thiele (1977) – Carabid beetles in their environments
Phenology – Egg load	Basedow (1994) – in Descender et al. Carabid Beetles – ecology and evolution
Microclimate – Emergence pattern	Holland et al. (2007) – Bulletin Entomol Res 97
Microclimate – Egg-laying site availability	Tréfás & Van Lenteren (2004) – Proc Netherlands Entomol Soc Meeting 15

This model concept is unique in that it couples external to internal drivers. Thomas et al. (2006), for example, directly link environmental driving factors to walking behaviour, but assume that beetles will always respond to these drivers in the same way. The coupling that we make between external and internal drivers is useful when motivation of beetles changes through the year, which we consider very likely. After emergence from their overwintering site or from the pupal stage, female beetles are expected to be motivated for foraging. But later in the season, as eggs are maturing, motivation will change to find a suitable egg-laying substrate. And at the end of the season, beetles will be motivated to find suitable overwintering sites.

Experimental approach

The relationship between walking behaviour and the external and internal drivers mentioned above will be studied for two common carabid beetles which occur in arable land: *Pterostichus melanarius* and *Poecilus cupreus*. We selected these species because (1) they differ in their reproductive and overwintering strategies (summer *versus* winter larvae) and (2) because they are large enough to track with cameras in a laboratory setup. By comparing two species with contrasting reproductive and overwintering strategies we expect to gain greater insight in the seasonal variation on internal drivers.

Our first aim is to identify the environmental conditions which determine habitat quality for foraging and egg-laying. To do this we create arenas with two artificial habitats that are contrasting in one environmental condition. We will first test plant density, prey density and soil moisture content. By comparing prey encounter rate and the number of eggs laid in a non-choice situation we hope to quantify habitat quality with respect to foraging and egg-laying.

Our next aim is to see how the motivation of beetles changes in the course of the season. To assess motivation we place beetles in arenas that consist of one patch that is optimal for foraging and one patch that is optimal for egg-laying and measure walking behaviour and residence time in each patch. We will repeat this experiment during the season to see how the motivation of beetles changes. At this point we should be able to say to which environmental factors beetles respond at a particular time in the year. All experiments are carried out in observation arenas of about 6 m^2. This large size is needed to minimize edge tracking behaviour, which is typical in studies on carabids in arenas that are too small (Mols, 1993).

Expected outcomes and discussion

The research proposed here attempts to scale up individual walking behaviour of carabids to patterns in population density in the field. We aim at a model that predicts the spatial behaviour of a population of carabids in a small landscape mosaic of several hectares. Strong point of this model is that it accounts for a change in the response of beetles to environmental variables as the motivation of the beetle changes. This enables us to simulate walking behaviour from spring to autumn. The weak point is that we need to collect substantial information on the environmental variables to feed the model. To account for this we will only consider those environmental variables that are most relevant for walking behaviour to explain population distribution at our scale of interest in casu fields plus adjacent habitats.
Similar to results of Firle et al. (1998), we expect dispersal to be determined by different mechanisms at different scales. At a large scale covering several fields searching for hibernation sites may for example be the strongest determinant, but at the scale of a single field foraging and/or egg-laying may determine distribution patterns.

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