INTERFERENCE COMPETITION AND PATCH CHOICE IN FORAGING SHORE CRABS

Smallegange Isabel

Royal Netherlands Institute for Sea Research (NIOZ), Landsdiep 4, PB 59, 1790 AB Den Burg, Texel, the Netherlands
Present address: Max Planck Institute of Ornitology, Vogelwarte Radolfzell, Schlossallee 2, 78315 Radolfzell, Germany
E-mail: smallegange@orn.mpg.de

Understanding the foraging decisions and the mechanisms that underlie the dispersal behaviour of foragers is of central importance in answering questions aimed at assessing the processes that determine the spatial distribution of species. The studies in this thesis aim to contribute to answering the question 'why do predators forage where they forage?'.

While foraging, animals regularly compete over (access to) food in direct, aggressive interactions. These interactions deprive individuals of time that was otherwise available for foraging and this reduces their feeding rate: a process that has been termed interference competition. To formulate hypotheses on the strength of interference competition in relation to the presence of competitors and prey availability, the so-called generalized functional response model is used. The generalized functional response relates the per capita feeding rate of predators to the prey and predator (=competitor) density in a certain food patch. If the generalized functional response is known, one can subsequently derive predictions on how predators distribute themselves across patches of different quality using the theory of ideal-free distributions (IFD). This theory forms a widely used starting point for formulating hypotheses on the spatial distribution of foraging animals. IFD theory predicts the distribution of animals that are omniscient ('ideal'), and that experience no travelling costs ('free') while moving to the patch that maximises their feeding rate. In the first, and most basic IFD model, animals are assumed to be of equal competitive ability. In that case, ideal and free animals distribute themselves such that the per capita feeding rate – as defined by the generalized functional response – is equal and constant across patches. The per capita feeding rate is determined by the generalized functional response model that is used. However, various generalized functional response models have been presented in the literature, and each one results in a different prediction on the spatial distribution of foraging predators. This means that in order to understand why predators forage where they forage, firstly, detailed knowledge on the foraging behaviour, *i.e.* the generalized functional response, of predators is required. This notion has formed the key motivation for the work conducted in this thesis.

Critical to investigating the strength of interference competition in foraging predators and its effect on their choice of food patch is that prey densities are kept at a (almost) constant level. The reason for this is that, otherwise, effects of exploitation competition (the overall reduction of prey availability as more prey are consumed) obscure effects of interference competition. What is more, models of the generalized functional response and IFD models assume constant prey densities. Therefore, a novel experimental approach was developed to keep prey densities at an almost constant level (Chapter 5)

so that the interference competition and patch choice of shore crabs (*Carcinus maenas*) foraging on mussels (*Mytilus edulis*) could be studied.

The *first part* of this thesis work (Chapter 2, 3 and Box III) was concerned with investigating how shore crabs handle (*i.e.* break and eat) mussels, what sizes of mussels shore crabs prefer, and how many mussels of which size shore crabs can eat before being satiated. These studies were done to assure that in all subsequent experiments, shore crabs always foraged on mussels that they could handle easily and that were of a size close to what they prefer, without reaching satiation levels (as that would stop shore crabs from foraging).

In the *second part* of this thesis work, the generalized functional response was assessed for shore crabs of equal competitive ability (Chapter 5). Since, in shore crabs, competitive ability is strongly correlated with their size, this means that only shore crabs of equal size were used. Continuous observation of the foraging behaviour of equal shore crabs showed that they suffered interference competition as they lost foraging time while being engaged in agonistic interactions (remember that prey densities were kept at an almost constant level to reduce effects of exploitation competition). The strength of interference competition increased with increasing crab density. These results were used to construct behavioural models in which the foraging and agonistic behaviours as observed in Chapter 5 were defined. That is, a Markov chain was developed that describes the foraging process of a few predators of equal competitive ability moving from one state of the foraging process to the next (Chapter 6). Each state of the foraging process is a combination of behaviours that the predators can display, for example, two predators can be searching, one can be searching the other handling, or both are fighting. If one of two searching predators finds a prey item, the foraging process moves from the 'both are searching' state to the 'one is searching, one is handling' state. If the duration and frequency of each behaviour as defined in the Markov chain can be measured in behavioural experiments, these models can be parameterised and put to the test. This was done in Chapters 6 and 7 for shore crabs of equal competitive ability. The predictive power of the model is high as there was a good fit between predicted and observed feeding rates (Chapter 7).

Subsequently, the Markov chain was extended to describe the foraging process of two (equal) predators foraging on two food patches of different quality (different prey densities), assuming that crabs have no preference for either patch (Chapter 8). This Markov chain was used to formulate a null hypothesis on the distribution of two shore crabs across two food patches. Specifically, the null hypothesis gives (1) the per capita feeding rate of the shore crabs on each food patch and (2) the amount of time each shore crab spends on a patch if they have no preference for either patch. Also, an alternative hypothesis, the ideal-free hypothesis, was formulated and for that purpose the results of Chapters 5 and 9 were used to predict (1) on which food patch shore crabs stay and (2) what their per capita feeding rate is if they aim to maximise their feeding rate, taking patch quality and number of competitors present into account. The two predictions on patch choice (no-preference *versus* ideal-free) were tested in Chapter 8 (prey densities were again kept at a constant level), which showed that crabs maximised their feeding rate by taking prey from the best food patch, in line with the ideal-free hypothesis. However, crabs did not stay on the best patch, but adopted a 'take-away' strategy whereby they carried prey away to consume it on the poor patch,

away from the competitor and thereby reducing interference. As a result, the time spent on each patch did not differ from that expected under the no-preference hypothesis.

The *third part* of this thesis work focussed on predators that differ in competitive ability. Firstly, the generalized functional response was assessed for shore crabs that forage in the presence of competitors of unequal competitive ability (unequal size) (Chapter 9). The results of the experiments revealed that interference competition between foraging shore crabs was greatest between individuals of equal competitive ability. This observation, together with predictions from the field of game theory (Chapter 4), was the motivation to explore how this would alter conclusions of current IFD models, as they are based on the premise that individuals suffer interference the most from dominant (larger) competitors. To this end, the equal predators Markov chain (Chapters 6 and 7) was adjusted for the fact that interference is stronger between two equal predators while searching than between two unequal predators (Chapter 10). New insights were gained from the behavioural observations in Chapter 9. The rules of interference in shore crabs as determined from Chaptre 5 were therefore improved and the Markov chain differs from that used in part two. Parameterizing this new Markov chain proved difficult as not all state durations could be measured from the behavioural data of Chapter 9, and an alternative procedure was used to arrive at parameter estimates (Chapter 10). The Markov chain applies to a small number of predators. However, to assess how strong interference between equal competitors affects their ideal-free distribution, a behavioural model is needed that applies to a large number of predators. Therefore, the behavioural rules of the Markov chain on interference and foraging were used to develop a generalized functional response model (the two-phenotypes interference model) for a large number of subordinate and dominant predators (Chapter 10). Using the new parameter estimates, ideal-free predictions on patch choice were derived. The model predicts that over a large range of predator densities, predators distribute themselves in a mixed manner with a larger share of dominants on the better patch, but with complete overlap of feeding rates of dominants and subordinates across patches. This contrasts with the predictions from many IFD models, where individuals suffer most from dominant competitors, which results in complete or partial segregation of the predator population by competitor type across food patches. The IFD prediction from Chapter 10 was tested in the laboratory (Chapter 10) and in the field (Chapter 11). In the lab, a large group of subordinate (small) and dominant (large) crabs foraged on two large mussel patches. Crabs, however, did not conform to the ideal-free assumption of omniscience, and the ideal-free prediction could not be tested. In the field, it was assumed that the quality of sampling sites was set by the abundance of brown shrimps (*Crangon crangon*: a preferred prey species). The observed spatial distribution of crabs pointed at a mixed, ideal-free distribution in line with the model prediction: expected feeding rates of dominant and subordinate crabs were similar across sampling sites at three intertidal mudflats in the western Wadden Sea (Chapter 11). However, the actual foraging behaviour of crabs was not observed and alternative hypotheses, such as that foraging decisions are determined by reducing the risk of predation by con- en heterospecifics, should also be considered. Because the distances between adjacent food 'patches' (*i.e.* sampling sites) in the field were large (3, 100 or 500m), a discrepancy between food intake and time spent in a patch is not expected, as was observed in the lab study where patches were immediately adjacent to each other (Chapter 8).

Has this thesis work increased the understanding of the processes that determine the spatial distribution of foragers? The results presented in this thesis show the impact of interference competition in foraging shore crabs and the relationship between prey availability and presence of others on the choice of food patch. New insights have been gained, such as the 'take-away' strategy, and current generalized functional response models have been improved. However, no hypothesis formulated in this thesis work on the foraging behaviour of predators across different food patches has unequivocally been confirmed. Furthermore, in this thesis work, assumptions have been made that may create (unforeseen) pitfalls, which are discussed in the final chapter, Chapter 12. These pitfalls, together with insights from the results of this thesis work, give rise to future lines of research that are outlined in Chapter 12. If pursued, they will contribute further to answering the question 'why do animals forage where they forage', and deepen the understanding of the processes that determine the spatial distribution of species such as shore crabs.