

INTERFERENCE COMPETITION AMONG FORAGING WADERS

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Competition is among the most studied topics in ecology, both theoretically and empirically. Nevertheless, understanding of competition is still wanting; ecologists are not quite able to tell why or to predict how much competing animals suffer from mutual interactions. This thesis strives to contribute to understanding of competition by studying the mechanisms of interference competition among waders (Charadrii), foraging in intertidal areas. It attempts to extend previous work by applying an experimental approach to the empirical study of interference competition and an evolutionary approach to its theoretical study.

The experiments presented in this thesis yielded the following results:

1. Chapter 2 reveals that (1) interference effects on intake rate are different for red knots (*Calidris canutus*) and ruddy turnstones (*Arenaria interpres*), (2) that the mechanistic basis of interference effects differed between these two species, but (3) that in neither of the two species interference effects resulted from kleptoparasitism (i.e. the stealing of food items), which is the most widely discussed interference mechanism.

2. Chapter 3 shows that the extent to which captive turnstones suffer from interference competition depends on both the spatial distribution of food and the relative social dominance status of focal individuals. When food is spatially clumped, interference competition may arise from the monopolisation of food clumps, and interference effects may be unrelated to the amount of agonistic behaviour. Chapter 4 shows that the spatial distribution of food affects the amount of agonistic behaviour and the distribution of free-living turnstones, but it does not affect the time focal individuals spent digging for food, which is taken as an approximation of intake rate.

3. Chapter 5 shows that the extent to which captive turnstones suffer from interference competition depends on the distribution of food and on the foragers' social dominance status (as before), but also on the divisibility of food, which is one of the differences between food items (indivisible) and food clumps (divisible).

Thus, interference competition among foraging waders need not result from the stealing of food items, but may also result from interactions over food clumps, and these two mechanisms may differ in a way that is essential to the interference process. The theoretical chapter of this thesis (chapter 6) reveals that models of interference competition have not yet reached consensus about the kinds of interference behaviour that can be expected to evolve. Although evolutionary models of interference competition appear to be similar, they yield strikingly different predictions regarding the evolutionary stability of various interference strategies. To unify previous approaches, a systematic event-based description of the foraging process is presented and the use of techniques from Adaptive Dynamics theory is promoted. Through a critical discussion of the setup, the assumptions and the way of analysis of some evolutionary models of

interference competition, crucial assumptions and potential pitfalls in modelling the evolution of interference behaviour are identified.

Together, these experimental and theoretical results contribute to a mechanistic and evolutionary understanding of interference competition. At the same time, they make it clear that we cannot claim having reached such an understanding yet. This implies that it still is premature to base models of population dynamics on presumed knowledge of the interference process.