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RESPONSES OF AN AVIAN PREDATOR TO VARIATIONS IN PREY DENSITY AT A TEMPERATE LATITUDE

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Abstract. Fluctuating prey populations and their effects on avian predator population dynamics have been studied particularly at high latitudes, where prey populations, especially microtines, are known to be cyclic; raptors show both numerical and functional responses to variations in their prey. In this paper, we investigate the response of a migratory raptor (Montagu's Harrier, *Circus pygargus*) to variations in abundance of its main prey (common vole, *Microtus arvalis*) in France. We document multiannual fluctuation in the abundance of common voles. The numerical response of Montagu's Harrier to this variable food supply was studied using breeding parameters (breeding density, breeding phenology, and various measures of breeding success). Breeding density and mean clutch size were strongly correlated with spring vole abundance, whereas mean brood size at fledging was correlated positively with summer vole abundance. The mechanism involved in the numerical response of Montagu's Harrier indicates that dispersal and colonization by yearlings may be more important than natality per se. Pellets collected between 1986 and 1997 were used to determine the functional response of Montagu's Harrier to variations in vole abundance. In terms of biomass, Montagu's Harrier diet consisted mainly of voles (33.7–86.6%, between 1986 and 1997). Vole biomass in pellets was closely related to vole abundance estimated by trapping. A type II functional response was detected, with satiation at high prey density, as the shapes of many relationships between breeding parameters and vole abundance were more curvilinear than linear. Our results fit the pattern of relationships between predators and cyclic prey found in Fennoscandia, in which specialist predators show a strong numerical response, although at such a temperate latitude, a more pronounced functional response might have been expected.

Key words: Circus pygargus; *common vole; cyclic prey; Fennoscandia; functional response; microtine rodent;* Microtus arvalis; *Montagu's Harrier; numerical response; predator; small-mammal cycles; variable prey density.*

INTRODUCTION

The relationships between predators and variations in prey density have been the subject of many studies. Solomon (1949) suggested that these relationships were of two types, numerical and functional. The numerical response is the relationship between the numbers of predators and the numbers of their prey, whereas the functional response describes how the rate of prey capture varies with prey abundance (Andersson and Erlinge 1977). Under a numerical response, the predator adapts its breeding effort or its numbers to the numbers of the prey, through differential natality or emigration (usually without time lags). The functional response is determined by other life history traits of the predator, or its foraging or social behaviors (Andersson and Erlinge 1977, Village 1981, Korpimäki and Norrdahl 1991). Empirical and experimental studies have revealed that three types of functional response exist, according to the nature of the relationship between predation rate and prey density (Holling 1959): linear (type I), convex (type II), and concave or sigmoid (type III). Studies of invertebrates have shown that predators that can switch to alternative prey are more likely to produce sigmoidal functional responses; this has also been shown in vertebrates (Keith et al. 1977). Functional response curves of avian and mammalian predators are usually convex (Murdoch and Oaten 1975, Keith et al. 1977, Linden and Wikman 1983, Korpimäki and Norrdahl 1991, Dale et al. 1994), although linear responses have sometimes been documented (Korpimäki and Norrdahl 1989, 1991; review in Boutin 1995).

Raptors show both numerical (Newton 1976, Phelan and Robertson 1978, Smith et al. 1981, Korpimäki and Norrdahl 1989, 1991) and functional responses (review in Sonerud 1992) to variations in food supply. Interestingly, both response types have been recorded in the same species, either at different times in the same area, or in different localities (Luttich et al. 1971, Phelan and Robertson 1978). Two predator strategies have been identified that differ in their reaction to variations of prey densities, and possibly in their effects on prey

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