CHAPTER 7
SPECIALIST–GENERALIST COMPETITION
IN VARIABLE ENVIRONMENTS; THE CONSEQUENCES
OF COMPETITION BETWEEN RESOURCES

PETER A. ABRAMS

Department of Ecology and Evolutionary Biology, University of Toronto, 25 Harbord St. Toronto,
Ontario M5S 3G5, Canada
Phone: 416-978-1014 Fax: 416-978-5878 E-mail: abrams@zoo.utoronto.ca

7.1 Abstract ............................................. 133
7.2 Introduction ........................................... 134
7.3 When and Why are Specialists and Generalists Able to Coexist on Two Resources? . . . . . 137
  7.3.1 Model 1: Fixed preferences ................................ 138
  7.3.2 Model 2: Adaptive change in the generalist’s preferences ........................... 143
7.4 How Do Coexisting Specialists and Generalists in Variable Environments Respond to Altered
  Mortality of One of these Species? ........................................ 146
  7.4.1 Models with inflexible foraging by the generalist ................................. 147
  7.4.2 Models with behavioral switching between resources by the generalist .......... 149
7.5 Discussion ........................................... 154
7.6 Acknowledgments ........................................ 155
7.7 Literature Cited ......................................... 155

7.1 ABSTRACT

Consumer-resource models have long been employed to help understand competition
between consumers, but the resources have usually been assumed to be independent
of each other. The impact of competition between resources is explored for a case in
which two specialists and one generalist compete for two nutritionally substitutable
resources. Coexistence of all three consumers requires that the relative abundance
of the two resources fluctuates over time. The conditions allowing coexistence of
all three consumer types is generally broadened considerably by the presence of
competition between resources. In addition, competition between resources usually
increases the density of the generalist consumer relative to the specialists. These

David A. Vasseur and Kevin S. McCann, The Impact of Environmental Variability on Ecological Systems,
133–157. © 2007 Springer.
results are due to the fact that the generalist persists by “consuming” negative covariance between resources, and competition between the resources increases the negative covariance in the absence of the generalist. The densities of the competing consumers often respond in counterintuitive ways to mortality imposed on one of the consumers. Frequently, the mean population size of one consumer is very insensitive to its increasing mortality over a broad range of mortality rates, but abruptly goes extinct when mortality surpasses a threshold value.

**Keywords:** competition, specialist, generalist, coexistence.

### 7.2 INTRODUCTION

During the 1970s several researchers discovered that sustained fluctuations in resource abundance could allow two or more species to coexist on a single resource (Stewart and Levin 1973; Koch 1974; Armstrong and McGehee 1976, 1980; Hsu et al. 1978; Levins 1979). Most experimental and theoretical work on exceptions to the “competitive exclusion principle” since then has focused on systems in which a single resource is the subject of competition. In a recent review, Chesson (2000) noted that very little was known about systems in which consumers competed for two or more variable resources. The few studies that have investigated competition for two or more resources (Huisman and Weissing 1999, 2001, 2002) have investigated a narrow range of models, and have assumed that the resources did not affect each other’s growth rates. The present chapter was largely motivated by a desire to determine the consequences for competitive coexistence of more species than resources in nonstationary systems when: (i) there is more than a single limiting resource; and (ii) the different resources interact with each other. This chapter will be restricted to the simplest multi-resource model, namely two resources that are nutritionally substitutable for their consumers. It will focus on the impact of competition between the resource populations on the interaction of the consumers that are competing for those resources. The framework with two substitutable resources builds on other recent studies of competition, coexistence, and coevolution in this framework (Abrams 2006a,b,c). Investigating the effect of resource competition on the interactions of consumers that share those resources was motivated by a series of articles by John Vandermeer (1980, 2004), showing that resource competition could greatly alter conditions for the coexistence of consumers for models in which the number of consumers was assumed to be less than or equal to the number of resources.

The work described here builds upon previous 1- and 2-resource models of competition for resources having temporal fluctuations in abundance, so it is useful to begin by reviewing some of the conclusions reached by that work. Analysis of the conditions required for coexistence of two species on a single resource suggests that endogenous consumer–resource cycles are more likely to lead to coexistence than is environmental forcing of resource growth (Abrams 2004), and that coexistence