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Original article

Resource partitioning in freshwater turtle communities: A null model meta-analysis of available data

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ABSTRACT

Resource partitioning is one of the most intensely studied issues in ecology since the mid-1900s, nonetheless this issue has never been examined in detail for several important animal groups, including the freshwater turtles. In this paper I re-analyze by null models several studies on resource partitioning by freshwater turtles published in the peer-reviewed literature. These studies originated from all continents and from a variety of climatic and habitat conditions. I used data given in the original papers to recalculate dietary overlap between species. Then, the true datasets were compared to randomly generated datasets produced by 3×10^4 Monte Carlo permutations, by using two different randomization algorithms (RA2 and RA3 of Lawlor, 1980). Datasets were inspected to find non-random structure of the various communities along four resource dimensions: macro-habitat, micro-habitat, food, and time. Based on my meta-analysis, I concluded that the micro-habitat resource is the most important dimension (it was the resource partitioned in nearly 80% of the study cases), followed by the food resource dimension (nearly 70%), whereas macro-habitat and time were clearly less important. In relation to micro-habitat dimension, the selection of basking site typology is perhaps the main aspect of the microhabitat niche to be partitioned. Logistic regression models indicated that the presence of a resource partitioning structure in the dataset was influenced only by matrix size, and not by number of species, continent, presence of substantial body size differences among coexisting species, or tropical versus non-tropical origin. A combination of causes may explain the observed patterns: interspecific competition is likely important in shaping several turtle communities, but intrinsic and extrinsic constraints and predation are also relevant.

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1. Introduction

Few patterns in community ecology have been documented as widely as resource partitioning, that is how sympatric species differ in their use of available resources (e.g., Schoener, 1974; Roughgarden, 1976, 1983). Resource partitioning patterns may generally derive from the interaction of some categories

of causes, including predation, extrinsic and intrinsic constraints on an organism's performance, and interspecific competition (e.g., see Toft, 1985; Barbault, 1991; Barbault and Stearns, 1991, etc.). Thus, the main scopes of resource partitioning studies are not only to describe the patterns as they occur in the living communities, but also to understand factors causing these patterns (e.g., Schoener, 1977).

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One problem with resource partitioning studies is that they differ tremendously among different organism groups in both patterns and causes, and thus generalization is often difficult. In ectothermic vertebrates that have been recently reviewed, resource partitioning is a widespread phenomenon and is generally due to interspecific competition in snakes (Luiselli, 2006a), whereas it is much rarer and generally not due to competition effects in terrestrial turtles (Luiselli, 2006b). The main causes of this tremendous variation in resource partitioning patterns among living communities of even relatively closely related animals are that competition is not equally intense at all climates and latitudes (being generally stronger in tropical than in temperate climates, Pianka, 1966; Rhode, 1992; Luiselli, 2006a), and also that there are several ways in which animals could compete, and the definition of competition is not univocal (e.g., Milne, 1961; Schoener, 1974, etc.).

Another problem with poor understanding of patterns and causes of resource partitioning is that there are many studies for some groups of animals and very few for many others. Regarding the herpetofauna, 51.1% ($n = 88$) of studies reviewed by Toft (1985) were relative to lizards, 18.2% to amphibian larvae, and just a very minor percentage was relative to each of the other groups. Turtles, including both terrestrial and aquatic species, accounted for just 2.3% of the total number of studies. Since Toft's (1985) review the studies on resource partitioning in animals, and in ectothermic vertebrates as well, have greatly improved in terms of both number of case studies and variety of organisms investigated, and some taxa that were poorly studied 20 years ago are currently well studied and even model organisms for evolutionary ecology studies (Shine and Bonnet, 2000). With regard to freshwater turtle community ecology, in the last 20 years several studies have been published in the international literature (Bodie et al., 2000; Cadi and Joly, 2000, 2004; Conner et al., 2005; Dreslik et al., 2005), but no synthesis has been attempted to search for general patterns and causes of resource partitioning. In this paper I performed an analysis of all published data on resource partitioning patterns in freshwater turtle communities. Where possible, I re-analysed by null models (Gotelli and Graves, 1996) the original datasets to inspect whether the various communities were (non-)randomly structured. Despite that fewer studies have been published on resource partitioning of freshwater turtles than on lizards or snakes, we may now at least understand the main trends, given that those studies came from all continents, from both tropical and temperate climates, and are relative to nearly all the main turtle families (see below). My aims with this review are: (i) to explore resource partitioning patterns in freshwater turtles on the various continents; (ii) to identify what are the most important resource dimensions for freshwater turtles world-wide; (iii) to understand what causes may be responsible for observed resource partitioning patterns; and (iv) to address some recommended areas for future research.

2. Methods

For this meta-analysis I used only studies published in peer-reviewed international journals or in university dissertations

that: (i) explicitly tested resource partitioning and interspecific competition hypotheses in freshwater turtle communities; and/or that (ii) provided datasets fully re-analyzable by statistical procedures (see below). I separately analyzed studies that addressed macro-habitat and micro-habitat niche aspects of the communities under study in accordance with earlier reviews (e.g., Toft, 1985). In order to define macro- and micro-habitats in this paper, I here use the study by Barko and Briggler (2006) as an example. Macro-habitat types in this study are open side channels and main channel borders versus tributaries and closed side channels; micro-habitat types are different basking sites, areas with different vegetation in water and/or on banks, and areas with different substratums available. In general, for my analysis I used the same micro- and macro-habitat types presented by authors in their original articles, assuming that the most accurate scale to distinguish between micro- and macro-habitats for turtles at each study area should derive from authors' expertise and familiarity with their own study sites. I included in the analysis studies considering all important resource dimensions (i.e., habitat, food and time, see Pianka, 1986) and those deliberately selecting certain dimensions although others may be important. However, in order to understand which of the resources are the most important for turtle communities, I calculated for each resource dimension the relative percentage of studies demonstrating that it is important and then compared the percentages of the various resource dimensions.

2.1. Null models and statistical procedures

Datasets were inspected to find non-random structure of the various communities along four resource dimensions: macro-habitat, micro-habitat, food, and time. To evaluate whether each turtle community was structured randomly or not, I contrasted the actual data matrix as given in the original literature source with random "pseudo-communities" generated by Monte Carlo simulations (Gotelli and Graves, 1996). Resource items data were parameterized as present or absent. Since too many zeroes in the matrices might distort the error levels while too often rejecting the null hypothesis of lack of structure, I used the option available in EcoSim to fix zeroes, i.e. retaining the zero states in all simulations. This was also justified because the different sizes of the turtles within each community might justify a fixing of zeroes (Pianka, 1986). Pianka's (1986) overlap formula was calculated for all communities, and the original species utilization matrices from which Pianka's overlap was calculated were randomized by shuffling the original values among the resource states. I used two randomization algorithms (RA2 and RA3) of Lawlor (1980), as they are particularly robust for niche overlap studies (Gotelli and Graves, 1996). RA2 tests for structure in the generalist-specialist nature of the resource utilization matrix by conserving guild structure, but destroying observed niche breadth (Gotelli and Graves, 1996). RA3 tests for guild structure by conserving niche breadth for each species, but destroying guild structure manifested by the zero structure of the resource utilization matrix (Gotelli and Graves, 1996). For each pair of species, 3×10^4 random Monte Carlo permutations were generated. This number of permutations is enough to avoid algorithm biases in calculations (Lehsten and Harmand,

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