

Nonadditive interactions between animal and plant diet items in an omnivorous freshwater turtle *Trachemys scripta*

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Abstract

Nonadditive interactions occur when diet items interact with one another such that the net energy or nutrient gain from a mixed diet differs from that predicted by summing the gains from individual diet components. We quantified nonadditive effects between duckweed, *Lemna valdiviana*, and grass shrimp, *Palaemonetes paludosus*, in the freshwater turtle *Trachemys scripta*. We fed turtles 100% duckweed, 100% shrimp, and two mixed diets containing 67% duckweed, 33% shrimp and 14% duckweed, 86% shrimp (dry matter basis). During each feeding trial, we measured intake, digestibility, and transit time of the diet, and upon conclusion, short-chain fatty acid concentrations in turtle digestive tracts. Digestibility was lower on the 67% duckweed diet, but higher on the 14% diet. These apparent nonadditive interactions may be due to differences in transit time of duckweed and shrimp. We believe this is the first evidence of two diet items producing opposing nonadditive effects when fed in different ratios.

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1. Introduction

Dietary mixing is widespread among animals, commonly occurring in many vertebrate and invertebrate species (Robbins, 1993; Coll and Guershon, 2002). Nonadditive effects between diet items may play an important role in the selection of mixed diets, particularly for diet items that differ radically from each other in nutritional composition or in how they are processed in the digestive tract (Bjorndal, 1991; Bozinovic and Martínez del Rio, 1996). These effects occur when diet items interact with one another such that the net energy or nutrient gain from the mixed diet differs from the net gain predicted by summing the gains from individual diet components. Although many studies have acknowledged the potential importance of nonadditive effects in their study species (Campbell and MacArthur, 1996; Nagy et al., 1998; Spencer et al., 1998; Chen and Lue, 1999; Durtsche, 2000), few have tested for or quantified these effects (Table 1).

The concept of nonadditive effects was first demonstrated in studies of domestic livestock nutrition. Like many herbivorous wildlife species, livestock, such as cattle, use microbial gut symbionts to digest plant material. These symbionts ferment plant cell wall components and produce waste products in the form of short-chain fatty acids (SCFA), which the host absorbs and uses as an energy source. Nonadditive effects found in livestock often result from alterations in microbial fermentation. For example, adding grain to a forage diet depresses digestibility because gut symbionts preferentially attack the easily fermentable grain carbohydrates rather than the structural carbohydrates of the forage. This rapid fermentation produces high concentrations of SCFAs that lower pH of the fermentation chamber and create an unfavorable environment for symbionts (Schneider and Flatt, 1975). However, if urea and a small quantity of easily fermented carbohydrate are added to forage, digestibility increases. This increase is due to extra nitrogen from the urea and readily available energy from the carbohydrate stimulating growth of the microbial population, which can then ferment the forage more efficiently (Pond et al., 1995).

Nonadditive effects have been demonstrated in a diverse array of wild species including insects, turtles, birds, ungulates, and rodents (see Table 1 for summary and references). In some

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Table 1
Summary of studies investigating nonadditive dietary effects in wildlife

| Diet items | | Study species | Type of interaction | Proposed mechanism | Source |
|---|--|--|---------------------|---|-------------------------------------|
| Fungus (species not given) | Wood (species not given) | Termites (species not given) | + | Ingestion of fungus provided cellulytic enzymes which facilitated digestion of plant parts | Martin and Martin, 1978 |
| Browse stems (<i>Vaccinium</i> sp.) | Grass hay (<i>Bromus inermis</i>) | Elk (<i>Cervus elaphus</i>) | + | Transit time of browse increased transit time of grass, facilitating fiber digestion | Baker and Hobbs, 1987 |
| | | Mountain sheep (<i>Ovis canadensis</i>) | + | Same as above for elk | |
| Fungus (species not given) | Wood (species not given) | Cerambycid beetles | + | Ingestion of fungus provided cellulytic enzymes which facilitated digestion of plant parts | Kukor et al., 1988 |
| Peach palm pollen (<i>Bactris gasipaes</i>) | Palm trichomes (<i>B. gasipaes</i>) | Beetle (<i>Cyclocephala amazona</i>) | + | Ingestion of highly lignified trichomes crush pollen allowing it to be digested | Rickson et al., 1990 |
| Duckweed plant (<i>Spirodela polyrhiza</i>) | Beetle larvae (<i>Tenebrio</i> sp.) | Yellow-bellied turtle (<i>Trachemys scripta</i>) | + | Nitrogen in larvae stimulated growth of gut microbial population which digested plant fiber more efficiently | Bjorndal, 1991 |
| Fungus (<i>Boletus edulis</i>) | Insect larvae (species not given) | Rodent (<i>Abrothrix longipilis</i>) | + | Nitrogen in larvae stimulated growth of gut microbial population which digested fungus carbohydrates more efficiently | Bozinovic and Muñoz-Pedrerros, 1995 |
| Pollen (<i>Opuntia echios</i>) | Nectar (<i>O. echios</i>) | Cactus finch (<i>Geospiza fortis</i>) | + | Nectar stimulated germination of pollen in the crop, facilitating digestion | Grant, 1996 |
| | | Medium ground finch (<i>Geospiza scandens</i>) | + | Same as above for cactus finch | |
| Millipedes (<i>Alloporus</i> sp.) | Kale leaves (<i>Brassica oleracea</i>) | Hingeback tortoise (<i>Kinixys spekii</i>) | – | Transit time of kale reduced transit time of millipedes | Hailey et al., 1998 |
| Milkweed flowers (<i>Asclepias syriaca</i>) | Milweed foliage (<i>A. syriaca</i>) | Beetle (<i>Tetraopes traophthalmus</i>) | – | Secondary compounds in foliage depressed floral digestion | Matter et al., 1999 |
| Whiting (<i>Merlangius merlangus</i>) | Sprat (<i>Sprattus sprattus</i>) | Lesser black-backed gulls (<i>Larus fuscus</i>) | No effect | None given | Hilton et al., 2000 |
| | | Common guillemots (<i>Uria aalge</i>) | – | None given | |

cases, possible mechanisms underlying these effects mirror those found in domestic livestock. For example, Bjorndal (1991) found a positive nonadditive effect in yellow-bellied slider turtles, *Trachemys scripta*, fed a diet comprised of 77% duckweed, *Spirodela polyrhiza*, and 23% *Tenebrio* larvae (dry matter basis). Adult yellow-bellied slider turtles are opportunistic omnivores that feed primarily on aquatic plants (Parmenter and Avery, 1990), and the ratio of plant to animal material in that study approximated that consumed by a wild population of adult *T. scripta* (Bjorndal, 1991). Bjorndal (1991) hypothesized that the positive nonadditive effect between duckweed and insect larvae was due to nitrogen in the larvae stimulating growth of the microbial symbiont population. She proposed this hypothesis because *T. scripta* use microbial gut symbionts to digest plant material (Bjorndal and Bolten, 1993) and because the cell wall, or fiber, component of the diet was most affected by the nonadditive effect.

The inclusion of animal material in a plant diet, however, does not consistently produce a positive nonadditive effect. For example, an omnivorous tortoise, *Kinixys spekii*, experienced a negative nonadditive effect when fed a diet comprised of 74.2% kale, *Brassica oleracea*, and 25.8% millipedes, *Alloporus* sp. (dry matter basis) (Hailey et al., 1998). This negative effect was attributed to kale, with its relatively short gut transit time, decreasing millipede transit time, thus depressing digestibility. Studies of *K. spekii* and *T. scripta*

(Bjorndal, 1991) demonstrate that plant and animal diet items do not always interact in similar ways. Additionally, studies of domestic livestock nutrition have demonstrated that the magnitude of a nonadditive effect can vary with different ratios of diet components (Van Soest, 1994). The direction of the effect could also vary, although that has yet to be demonstrated. Because nonadditive effects can significantly alter diet value, better knowledge of these effects is required to understand more completely the nutritional ecology of animals consuming mixed diets.

The purpose of this study was to quantify nonadditive effects in *T. scripta*, using previously untested diet items, duckweed, *Lemna valdiviana*, and freshwater grass shrimp, *Palaemonetes paludosus*. We performed a series of feeding trials in which we fed adult turtles 100% duckweed, 100% shrimp, and two mixed diets containing either 67% duckweed and 33% shrimp or 14% duckweed and 86% shrimp (dry matter basis). During the feeding trials, we measured intake, digestibility, and transit time of the diets. At the conclusion of each trial, we measured SCFA concentrations in the digestive tracts of turtles on each diet. The results of these feeding trials allowed us to (1) determine if nonadditive effects exist between duckweed and shrimp, (2) assess if any existing nonadditive effect varied with the ratio of plant to animal material, and (3) evaluate possible mechanisms underlying these effects.

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