African mammals, foodwebs, and coexistence

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In the 65 million years since a mass extinction led to the demise of dinosaurs, evolution has generated amazingly diverse and complex foodwebs on each continent (1). These foodwebs contain hundreds to thousands of interacting species, each linked to other species either by feeding on them or by being fed on by them. However, it has been difficult to determine consumer diets across seasons, individuals, and space, and especially hard to quantify the strengths of these linkages in all but the simplest foodwebs. These issues have limited the ability of ecologists to understand how foodwebs are structured, how so many interacting species can coexist, and how the patterning and strengths of these linkages determine the stability of foodwebs (2). The use of next-generation sequencing is emerging as a key tool for quantifying, with fine resolution, the diet composition of consumers (3). By using these high-throughput techniques on fecal samples from large African herbivore species to quantify their diets, Kartzinel et al. (4) provide important insights into foodweb structure and coexistence in one of the few remaining terrestrial foodwebs that still has its full complement of large mammals.

In particular, Kartzinel et al. (4) extracted DNA from the feces of seven large African herbivores—the African elephant, impala, two species of zebra, buffalo, Boran cattle, and dik-dik—within a 150 km^2 portion of Kenyan savanna (Fig. 1). To determine diets of each species, they obtained from 27 to 52 fecal samples per species during a single season. DNA metabarcoding allowed them to quantify the relative dietary abundances of about 100 different plant species or genera, thus demonstrating the efficacy of this approach for coexisting mammals. They found surprisingly strong dietary differences among these herbivore species. This dietary niche differentiation can explain the stable coexistence of these competing species.

An earlier study that used carbon isotopes in feces was able to quantify abundances of two major groups of plants, grasses, and browse, and showed that many (but not all) herbivore species were separated along a gradient defined by the ratio of these two plant groups (5). Kartzinel et al. (4) have provided the finest-resolution evidence to date demonstrating that each large African herbivore species consumes a suite of plant species different from the suite consumed by other cooccurring herbivore species.

Why is this so important? The work of Kartzinel et al. (4) suggests that the performance of a given herbivore species depends not on how much "forage" a grassland or savanna may contain but on the actual abundances of those particular plant species on which that herbivore specializes. For example, the plains zebra and Grevy's zebra both mainly eat grass and thus would seem to be strong competitors. However, Kartzinel et al. found that there were 14 grass species and a forb species upon which these two competitors were niche differentiated, with 10 of these plant species mainly eaten by Grevy's zebra and 5 mainly eaten by the plains zebra.

Why does this dietary differentiation lead to coexistence? Clearly, by eating different plant species, each herbivore species reduces the abundances of its own preferred food plant species more than it reduces the abundances of the preferred food for the other species. This dietary differentiation meets the classic ecological criterion for the coexistence of competing species: that each species inhibits itself more than it inhibits the other species. However, because of the multiple linkages and potential feedback paths in foodwebs, cause and effect relations are rarely so simple (6–9). These 15 plant species likely compete with each other. When Grevy's zebras are at high abundance, they will cause their 10 favored plant species to be rarer. The five plant species preferentially consumed by the plains zebra might then increase in abundance because of reduced competition, which would benefit the plains zebra. A similar process could cause high densities of plains zebras to benefit Grevy's zebras. These indirect effects, mediated by competitive interactions among plants for their own limiting resources (water, nitrogen, phosphorus, light, etc.), would enhance the ability of two seemingly close competitors to stably coexist. Indeed, the net effect of each of the zebra species on the other might actually become positive and form an "indirect mutualism" if the competitive interactions among the 15 plant species were strong (7).

Fig. 1. African mammals studied range in size from elephants (*Top*), to Grevy's zebra (*Middle*), to the dik-dik (*Bottom*). Images courtesy of Andrew Dobson (Department of Ecology and Evolutionary Biology, Princeton University).

Achieving a more mechanistic and predictive understanding of foodwebs is one of the major challenges facing ecology. A foodweb is a complex network influenced by the intensity of species interactions, which themselves quantitatively depend on the tradeoffs each species faces in dealing with top-down forces (e.g., from its predators or disease), bottom-up forces (from competition

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for growth-limiting resources), and feedback effects that propagate through the network. Generalist consumers, such as large herbivores, can affect distant parts of a food web, yet a detailed understanding of the interactions between generalist consumers and their food species was generally out of reach until the development of next-generation sequencing tools.

Dietary differentiation, should it prove to be of general importance in other mammalian foodwebs, could shed light not just on the present-day ecology of these foodwebs but also on the ecological constraints that may have structured the evolution of large mammalian herbivores and that perhaps determined which species were successful migrants between continents during the last 20+ million years.

Earth's large terrestrial mammals evolved on five continents but now mainly survive in Africa. Africa's high diversity resulted from land bridges that periodically allowed mammalian herbivores and predators that evolved on one continent to move to another. A variety of mammals that evolved in North America migrated to Asia and Africa, including camels, horses, and other grazing or browsing herbivore species and several scavengers and predators. Other mammals of African or Asian origin similarly migrated into North America. Despite apparent similarities among species, the resident and invading species coexisted (1, 10, 11). Such coexistence is also common following migration by mollusks, plants, and other taxonomic lines to new geographic regions (12–14).

The work of Kartzinel et al. (4) raises the interesting possibility that the species that were successful invaders had dietary preferences different from the established species on their new continent, and that such differences allowed both their invasion and their coexistence. After all, an invading species must be able to survive and reproduce on the resources left unconsumed by the species established in the shared habitat. There will generally be notable levels of unconsumed resources if an invading species has dietary preferences that are significantly different from those of the established species. Although we cannot go back in time, comparative studies of current diets of both herbivores and predators might

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shed considerable light on why some species were able to invade and coexist with, but not displace, the established species, and why other species were not able to invade, and yet also were not displaced by species that did invade their habitat.

The work of Kartzinel et al. (4) also raises many questions. For instance, what constraints and tradeoffs limit the breadth of diets and lead to specialization by herbivores? Are dietary choices mainly the result of how plant species meet the nutritional needs of an herbivore? Or do diets reflect spatial patterns of cooccurrence of various plant species? Or might the dietary choices of large herbivores be determined by the plant species that tend to cooccur in the sites that provide a given species of herbivore with its greatest protection from its predators?

Each terrestrial foodweb is a 1,000+ piece puzzle containing some subset of Earth's >300,000 species of vascular plants, >25,000 species of vertebrate herbivores, omnivores, and predators, and >1,000,000 species of herbivorous, predatory, parasitoid, and pollinating insects and arthropods (15). All organisms evolved in, and live in, such foodwebs, where, to survive, they must successfully compete for limiting resources and defend themselves from predators, parasites, and diseases. The next-generation sequencing approaches used by Kartzinel et al. (4) may finally allow us learn, at the level of individual species, how the constraints, tradeoffs, and feedback effects species experience in foodwebs interact to determine the diversity, functioning, and stability of Earth's most complex, and most threatened, terrestrial ecosystems.

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