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# Ecology: A revolution in resource partitioning

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**Resource partitioning stabilizes species coexistence but has long been difficult to measure. DNA metabarcoding reveals previously hidden dimensions of this problem and insights relevant for understanding and fostering coexistence — not just among wild carnivores, but also between carnivores and people.**

Perhaps the most fundamental question in ecology is how competing species coexist despite a limited supply of the resources they need to survive and reproduce. How do we explain the co-occurrence of two-dozen types of large grazing mammal intermingling on an East African plain, or the half-dozen carnivores that eat them? Why does one dominant competitor not exclude the rest? The solution to this puzzle has several pieces[1], the most important of which is that no two species use exactly the same resources in exactly the same place at exactly the same time. That is, differences in the ecological 'niches' of sympatric species stabilize coexistence by reducing the likelihood that one species will deplete the resources needed by another[2,3]. Although the importance of resource partitioning for the maintenance of biodiversity is well established, ecologists have a surprisingly weak grip on how it actually plays out among wild animals[4]. A new study in this issue of *Current Biology* by Xinning Shao, Meng Yao, Sheng Li, and colleagues[5] provides an unprecedented account of dietary niche partitioning by meat-eating mammals in the Mountains of Southwest China — a biodiversity hotspot hosting populations of Asiatic golden cat, leopard, snow leopard, Himalayan wolf, brown bear and other charismatic carnivores of conservation concern (Figure 1).

Few aspects of an animal's ecology are more basic than what it eats, so it might seem puzzling that dietary resource partitioning is so poorly understood. To understand why this is the case, consider those large grazers in Africa. They all eat grass, but which grass? There are over 200 grass species in the Serengeti, and some of them look similar enough to stump the world's best botanists. And as it turns out, these animals eat more than just grass; to varying degrees, they also eat the diverse herbs that grow amongst the grasses. As for getting close enough to see what exactly is going into the mouth of that crotchety Cape buffalo — you can always try. Lee and Martha Talbot, writing from Kenya in 1962, summed up the problem: "Six or more species of grass may occur within a square foot, and several species may be found growing in the same clump. Under these conditions even if one were to stand beside the animal, it would be difficult to identify which individual plants were being eaten"[6]. Researchers have strived mightily against these constraints for decades, with middling success[4]. Other types of animal present analogous challenges. When a lion tackles a wildebeest, it ain't subtle. But what do large carnivores secretly snack on when nobody is watching?

Attempts to assemble global databases on the feeding habits of wild mammals underscore the magnitude of the dietary data deficit. A 2014 study[7] scoured the literature and found rudimentary diet information — foods lumped into coarse categories such as 'invertebrate', 'mammal', 'fruit' and 'leaf' — for just 38% of the world's mammal species. This knowledge gap undermines ecology and conservation by obscuring the mechanisms of competition and coexistence, the structure of food webs, the evolutionary processes that shape foraging behavior, and the information needed to sustain endangered species both in the wild and in captivity[8,9]. For example, the study of ecological networks is booming, powered by sophisticated computational tools[10], yet it remains hamstrung by the fact that empirical data on feeding relationships are, for the most part, pathetic[4].

## A new wealth of diet data

Over the last decade, fecal DNA metabarcoding has emerged as a formidable tool for diet analysis[4]. By sequencing short fragments of DNA in

 

**Figure 1. Elusive carnivores give up their dietary secrets.**
Himalayan wolf *Canis lupus chanco* (syn. *C. himalayensis*), leopard (*Panthera pardus*), and snow leopard (*Panthera uncia*). In addition to being beautiful, these camera-trap images provided important data on each species' distribution across the study area in the Mountains of Southwest China biodiversity hotspot. (Photos: Sheng Li.)

fecal samples, researchers can reconstruct a nearly comprehensive picture of what an animal ate over the preceding few days. This approach is not infallible, but it represents a great leap forward in ecologists' ability to figure out who ate what without needing to capture or even get close to the animals. The few studies that have used fecal metabarcoding to analyze whole communities of animal species have provided powerful and often surprising insights into dietary niches. Large grazers in East Africa provide a case in point. Two species of zebra co-occur in central Kenya, the common plains zebra and the endangered Grevy's zebra. Both of these closely related equids almost exclusively eat grass, but each zebra eats grass species that the other does not, and the shared grass species are eaten by each zebra in different proportions[11–13]. Elsewhere, presumed strict grass eaters — such as Cape buffalo in Mozambique[14] and bison in Kansas[15] — have been found to subsist largely on forbs and small shrubs. These discoveries challenge deeply ingrained wisdom about what animals eat and the mechanisms through which resource partitioning emerges. A thorough reckoning is needed.

Shao and colleagues[5] used the game-changing metabarcoding approach to characterize prey partitioning in three different carnivore assemblages in the mountainous west of Sichuan Province in China. In total, they collected more than 1,000 scats from 17 species ranging in size from 0.1 kg (mountain weasel) to 240 kg (brown bear), a richness of carnivores rivaling that anywhere on Earth. By sequencing a diagnostic mitochondrial DNA marker, the authors were able to compile high-resolution diet profiles for the nine species represented by >35 samples, identifying 95 vertebrate prey taxa and 260 different predator–prey interactions.

## The species in the feces

At all three sites, sympatric species differed significantly in diet composition, adding to a growing weight of evidence that food partitioning is ubiquitous in animal communities and that molecular methods are essential for a full accounting of niche differences[11,16,17]. Although spatial separation of animals in this mountainous region contributed somewhat to their dietary differences, the study provides compelling evidence that resource partitioning also emerged at small scales. These differences, in turn, were structured in part by body size, with larger predators tending to take larger prey. That finding is not surprising but is nonetheless an important confirmation of the role of body size in creating niche differences and facilitating coexistence. Larger carnivores also ate less diverse diets, which is not immediately intuitive, given that larger animals should be able to subdue and eat a wider range of prey[18]; it nonetheless accords with expectations based on foraging theory, as big-bodied predators focused on the smaller number of prey species large enough to provide a substantial return on energetic investment. Body size did not explain all of the observed variation, however, suggesting that other factors also help to differentiate prey selection.

Further insight into prey preference was possible because the investigators quantified the relative abundance of major prey types, which enabled them to assess selectivity — that is, the pattern of use relative to availability. Analyzing selectivity is important for deep inference about resource partitioning, but it has rarely been achieved in metabarcoding studies (but see[14]), in part because it can be surprisingly difficult to match DNA retrieved from fecal samples with the corresponding species in the field[4]. Importantly, this analysis provided insights that may prove crucial to conserving the megadiverse and threatened large-mammal community at their westernmost study site, Shalulishan. Leopards were unique among the large carnivores in selecting tufted deer, Chinese goral, and mainland serow, all of which are globally threatened or near-threatened (as is the leopard). Brown bear uniquely selected musk deer, another endangered species. However, bear, wolf and dog all strongly selected for three domesticated species, yak, cattle, and horse. The authors attribute the persistence of large carnivores at Shalulishan, despite these depredations, in part to the "Tibetan cultural belief in wildlife protection." Yet a large literature on human–wildlife conflict attests that such tolerance only extends so far, and that conflict in many regions — including the Himalayas — is likely to intensify with climate change[19]. Proactive measures to mitigate and compensate for livestock consumption may therefore be necessary for Shalulishan to remain among the world's richest carnivore assemblages.

Beyond the important conclusions at the core of this study, the unrivaled dataset underpinning it is a valuable resource that can be mined for future syntheses — not to mention fascinating natural-history anecdotes that may likewise provide guidance for conservation policy. Snow leopard mainly eat blue sheep with some yak on the side, but pheasant is also on the menu, including the gorgeous and threatened Chinese monal. Wolf and bear occasionally snack on greater hog badger, itself a threatened carnivore with an unusual piglike snout. Other species in the study ate lizards, fish, and an array of birds in addition to large and small mammalian prey.

By sequencing environmental DNA, researchers are able to cut through some of the complexity that has long bogged ecology down. We need more studies like that by Shao and colleagues[5], along with centralized public repositories of dietary metabarcoding data to feed the study of network ecology[4]. Various other challenges remain. Quantitative interpretation of metabarcoding data is important for many inferences but remains tentative and in need of further refinement and validation[20]. Fecal DNA is silent about some aspects of species interactions, such as whether carnivores killed or scavenged their food. And although data on diet composition and resource partitioning are necessary for understanding competition and coexistence, they are not alone sufficient; for that, we need to harness the growing wealth of high-resolution dietary data to innovative experimental field research and modeling.

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