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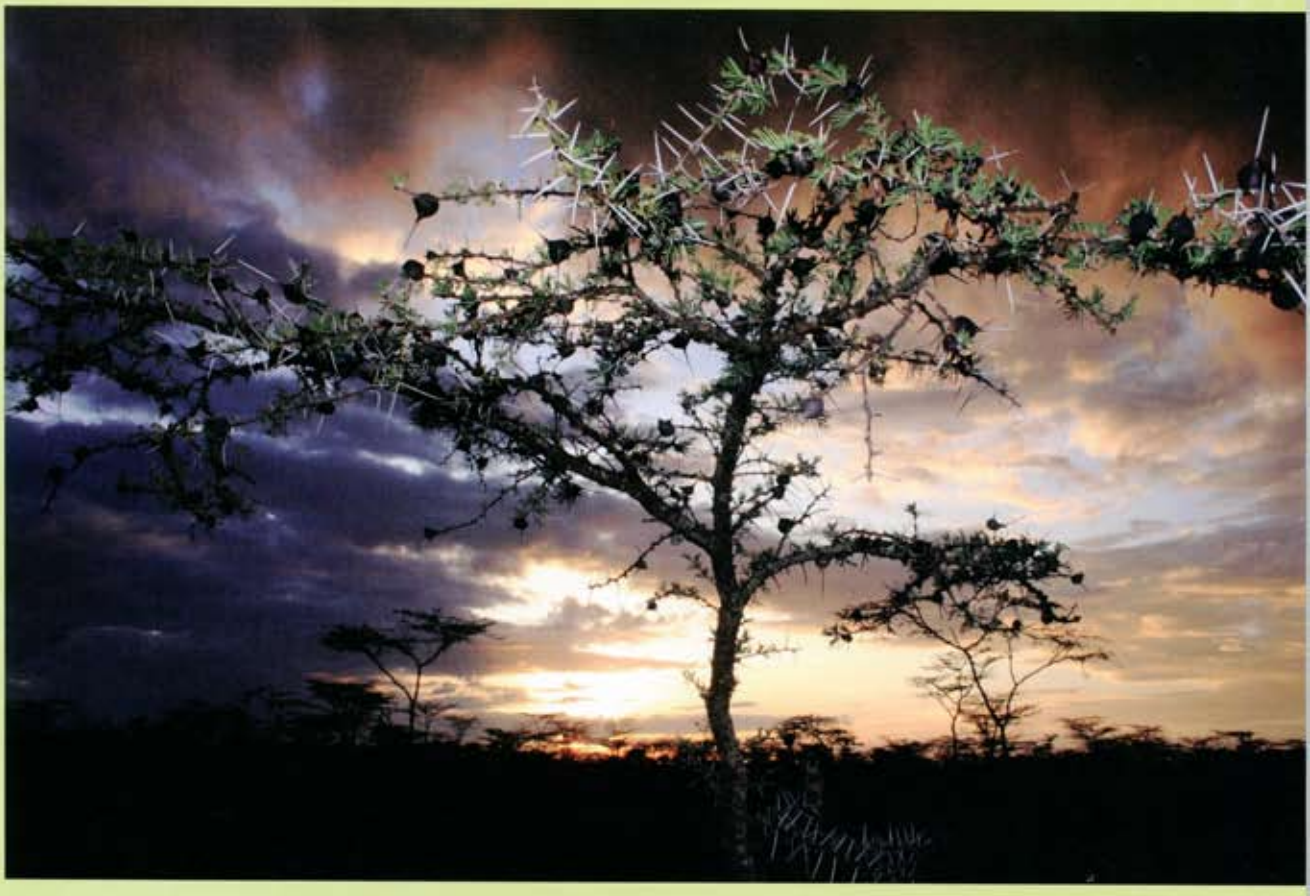

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LETTER

Coupling of canopy and understory food webs by ground-dwelling predators

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Abstract

Understanding food-web dynamics requires knowing whether species assemblages are compartmentalized into distinct energy channels, and, if so, how these channels are structured in space. We used isotopic analyses to reconstruct the food web of a Kenyan wooded grassland. Insect prey were relatively specialized consumers of either C_3 (trees and shrubs) or C_4 (grasses) plants. Arboreal predators (arthropods and geckos) were also specialized, deriving *c.* 90% of their diet from C_3-feeding prey. In contrast, ground-dwelling predators preyed considerably upon both C_3- and C_4-feeding prey. This asymmetry suggests a gravity-driven subsidy of the terrestrial predator community, whereby tree-dwelling prey fall and are consumed by ground-dwelling predators. Thus, predators in general couple the C_3 and C_4 components of this food web, but ground-dwelling predators perform this ecosystem function more effectively than tree-dwelling ones. Although prey subsidies in vertically structured terrestrial habitats have received little attention, they are likely to be common and important to food-web organization.

Keywords

African savanna ecosystems, allochthonous fluxes, dietary reconstructions, donor control, food-web stability, interaction strengths, predator–prey interactions, spatial subsidies, stable isotopes, trophic levels.

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INTRODUCTION

The importance of spatial fluxes of energy in food webs has been firmly established (Polis *et al.* 1997), and an increasing number of studies document their roles in linking aquatic and terrestrial habitats (Nakano & Murakami 2001; Cole *et al.* 2006; Catenazzi & Donnelly 2007), as well as distinct terrestrial habitats (Rand *et al.* 2006; Hawes 2008). Many of these examples fit the definition of 'spatial subsidies' proposed by Polis *et al.* (1997): asymmetric movement from one habitat to another of donor-controlled resources that increase the productivity of the recipient population. Such subsidies can have dramatic effects on species composition and trophic dynamics at landscape scales (Polis & Hurd 1995; Nakano *et al.* 1999). Polis *et al.* (1997) recognized that subsidies could also occur 'sympatrically' among patches of microhabitat; subsequent studies have demonstrated key linkages between benthic and pelagic and other habitats in aquatic systems, separated in some cases by scales of a few meters (Schindler & Scheuerell 2002; Vadeboncoeur *et al.* 2002). Within terrestrial ecosystems, however, subsidies operating over such small spatial scales have received little attention.

This gap might have important ramifications for food-web theory in terrestrial environments, just as the failure to recognize the magnitude of benthic-pelagic linkages obstructed progress in aquatic ecology (Vadeboncoeur *et al.* 2002). The broad appreciation of cross-boundary linkages notwithstanding, most theoretical investigations of food-web structure and dynamics do not consider spatial subsidies (but see, e.g., Huxel & McCann 1998; Fagan *et al.* 2007). The impossibility of accounting for all allochthonous inputs to a system at a landscape scale justifies this approach, to a certain extent. However, if subsidies are common and predictable at small spatial scales, then it should be possible to incorporate them more fully into food-web descriptions. Doing so will enable more realistic models with greater explanatory and predictive power – a high priority, given the importance of food-web structure in determining community stability (May 1972; Allesina & Pascual 2008) and key ecological processes (Montoya *et al.* 2003).

Empirical and theoretical arguments hold that higher-order consumers should couple food subwebs, thereby integrating distinct energy channels across habitats (McCann *et al.* 2005; Rooney *et al.* 2006). The presence of a subsidy, however, creates the potential for functional asymmetry among the predators in each habitat type: predators in the recipient habitat should be more effective couplers than predators in the donor habitat. We used carbon and nitrogen stable-isotope ratios to investigate a tropho-spatial linkage that seems likely to be ubiquitous, but that has been largely overlooked in the growing literature on spatially coupled food webs: gravity-driven transport of small consumers from tree canopies to the understory. We first utilized $\delta^{15}N$ values to help categorize consumers and establish patterns of tropic connectivity; after that, we used predator and prey $\delta^{13}C$ values to model energy flow among tree-canopy and grass-understory habitats.

METHODS

Study system and sample collection

We collected animal samples for this study during the 2007 and 2008 field seasons at the Mpala Research Centre (0°20′ N, 36°53′ E) in central Kenyan savanna. These sampling periods encompassed one rainy (June–August, 2007: 267.5 mm) and one dry (January–February, 2008: 22.4 mm) period in a system that receives an average of 500 mm rainfall per year. The study area is underlain by heavy-clay vertisol ('black cotton') soils that support limited plant diversity. The small (typically 2–3 m) myrmecophytic tree *Acacia drepanolobium* Sjøstedt constitutes > 97% of the overstory, while C_4 grasses (five dominant species) constitute *c.* 97% of the understory (Riginos & Young 2007; Riginos & Grace 2008). *Acacia* and grasses utilize distinct photosynthetic pathways (C_3 and C_4, respectively), and thus have distinct distributions of $\delta^{13}C$ values (Ehleringer & Monson 1993). C_3 photosynthesis discriminates more strongly against ^{13}C in atmospheric CO_2 than does C_4 photosynthesis, which results in an average difference of 16.1‰ between the $\delta^{13}C$ values of C_3 *Acacia* trees and C_4 grasses in our study area.

Acacia drepanolobium is inhabited by four species of symbiotic ants (Palmer *et al.* 2008). In this study, we examined only trees inhabited by the most common ant, *Crematogaster mimosae* Santschi. Trees inhabited by all four ant species, however, support assemblages of herbivorous and detritivorous insects, predatory arthropods, and often one or more individuals of the gecko species *Lygodactylus keniensis* Parker. *Lygodactylus keniensis* is small (*c.* 3.5-cm snout-vent-length), diurnal, and exclusively arboreal, and it is almost certainly the most abundant vertebrate in this system (> 1000 individuals ha^{-1} in places). Greer (1967) stated that individuals in northern Kenya consumed a wide variety of insects but avoided ants; Hardy & Crnkovic (2006) reported that individuals from central Kenya appeared to prefer beetles above other insect orders.

To obtain gecko samples for isotopic analysis, we captured adult geckos of both sexes in both seasons and removed a small amount of tissue from their autotomous tails before releasing them back onto their home trees. Gecko tissue samples (n = 37; see Table S1) were frozen and dried to constant weight at 60 °C prior to processing in the lab.

Arboreal arthropods were collected in both wet and dry seasons by misting tree stems and canopies with 0.6% alphacypermethrin from a backpack sprayer. Seventeen trees were selected across several locations several-hundred meters apart, subject to the conditions that the trees were 1.1–2.3 m tall (mean ± SD: 1.7 ± 0.25 m) and occupied by the ant *C. mimosae*. Prior to misting, we arranged white sheets beneath the canopies. We blew mist into each tree for 30 s and collected all arthropods falling onto the sheets during the subsequent 30 min, shaking trees to dislodge dead individuals. We attempted to analyse one or two individuals of each order represented in each sample and to ensure broad coverage across the morphospecies present in the total pool (n = 73; Table S1). We did not include *Acacia* ants in our analyses because these species subsist largely on tree-derived resources (preying only rarely on ground-dwelling arthropods: Palmer 2003), while workers to not appear to be prey for the predator species studied (Greer 1967; R. M. Pringle, personal observations).

Terrestrial arthropods were collected by sweeping the grass and deploying pitfall traps. Sweep-netted arthropods were collected in both the wet and dry seasons at each of 42 locations, whereas our pitfall samples were collected only during the dry season at each of 16 locations. Subsets of arthropods (n = 65 sweep netted, n = 18 pitfall trapped) were selected for isotopic analysis in an effort to ensure broad coverage across taxa, body sizes, and trophic levels (Table S1). All arthropods were frozen, identified at least to order and sometimes to family or genus, and dried to constant mass at 60 °C prior to processing in the lab.

For food-web analyses, we used five feeding and taxonomic groups: geckos and four groups of arthropods categorized on the basis of where they were collected (i.e. arboreal vs. terrestrial) and their trophic position (predator vs. non-predator, or 'prey') as inferred from basic natural history and analysis of $\delta^{15}N$ signatures. We were able to identify many arthropods with sufficient resolution to determine that they were herbivores (Phasmatodea; Acrididae; lepidopteran larvae; coleopterans of Curculionidae, Buprestidae, and Chrysomelidae, etc.). We examined the range of $\delta^{15}N$ values for a set of 46 known herbivores, which spanned −1.4‰–6.25‰ (excluding one phasmid with an anomalously high $\delta^{15}N$ = 7.7‰). We then compared the

$\delta^{15}N$ values of trophically ambiguous individuals (unidentified Hemiptera, carabid beetles, etc.) to the range of known herbivores, and all individuals with $\delta^{15}N \leq 6.25$ were categorized as 'prey.' Because we wanted to account for as much variation in resource consumption as possible, we treated individuals as independent samples. Thus, we analysed 25 arthropods collected from the same tree or sweep sample as another individual of the same taxonomic group. Relative to pooling individuals from the same location, assuming independence did not substantially affect mean $\delta^{13}C$ or $\delta^{15}N$ values but did increase the variance, suggesting that our results were not biased by non-independence of samples.

Acacia and grass (*Pennisetum* sp.) foliage samples ($n = 20$ each; Table S2) were collected in the same area during January and February 2007 (rainfall = 35.0 mm). Each *Acacia* sample consisted of fresh leaves from three adjacent trees; all trees sampled were 1–4 m tall, and all samples consisted of the youngest fully unfurled leaves on a branch tip. Grass samples also consisted of fresh leaves from three to five plants within *c.* 1 m^2. Samples were dried to constant mass at 60 °C immediately after collection.

Sample preparation and isotopic analyses

To remove surface contamination, gecko tail fragments were dipped in a 1 : 1 chloroform : methanol solution and wiped clean. Scale keratin was the target tissue for isotopic analysis; scales were scraped free with a scalpel. Approximately 0.8 mg of scales from each gecko were weighed into tin boats and analysed at the University of California Santa Cruz Stable Isotope Laboratory (UCSC-SIL; Thermo Finnegan Delta-Plus XP IRMS) or the University of Wyoming Stable Isotope Facility (UWYO-SIF; Thermo Finnegan Delta-Plus XP IRMS). To estimate instrument isotopic error, we included a protein standard every 12th sample for all runs at both labs; instrument error was always $< 0.2‰$ for $\delta^{13}C$ and $\delta^{15}N$. To validate combining datasets generated in two different labs, we verified that the absolute isotopic values of the protein standard were equivalent between labs. The $\delta^{13}C$ and $\delta^{15}N$ values in two replicate samples from each of seven individual geckos were within $0.5‰$ and $0.3‰$ of each other, respectively. We used atomic C : N ratios to determine whether other tissues (e.g., skin or fat) contaminated these scale samples. Most gecko samples ($n = 32$) had atomic C : N ratios of 2.9–4.0, which brackets the theoretical keratin C : N ratio of 3.4 (for mammalian α-keratin; O'Connell & Hedges 1999). Five samples had C : N ratios between 4.1 and 4.6, indicating some skin or fat contamination, but as we observed no correlation between C : N ratio and isotopic values (for $\delta^{13}C$: $r = -0.2$, $F_{1,35} = 1.7$, $P = 0.2$; for $\delta^{15}N$: $r = 0.08$, $F_{1,35} = 0.2$, $P = 0.6$), we included these individuals in our analyses.

For arthropods, protein (from muscle or cuticle) was the target tissue for stable isotope analysis. We preferentially drew samples from legs, but occasionally included head capsules if legs were too small (arthropod legs and head capsules are both highly proteinaceous body parts, with muscle and cuticle being main components of both). Several arthropods were too small to be analysed individually; in such cases ($n = 14$), samples consisted of body parts from two to six individuals of the same morphospecies (see Table S1). Arthropod samples were placed into glass vials and rinsed (30-min sonication) three times in a 1 : 1 chloroform : methanol solution to remove lipids. Dried 0.8-mg arthropod samples were weighed into tin boats and analysed at either UCSC-SIL or UWYO-SIF. Values of $\delta^{13}C$ and $\delta^{15}N$ for two replicate samples from each of 18 individuals were within $0.5‰$ and $0.7‰$ of each other, respectively. We used atomic C : N ratios to assess the relative contributions of protein and chitin to the sample $\delta^{13}C$ and $\delta^{15}N$ values. Most insect samples ($n = 149$) had C : N ratios of 2.5–4.0, which approximates the range of muscle protein (*c.* 3–4) and is much lower than the theoretical chitin atomic ratio of 6.9 (Schimmelmann & DeNiro 1986; Webb *et al.* 1997). Therefore, we inferred that the arthropod samples consisted primarily of protein. Five samples had C : N ratios of 4.1–4.3, but we included them in analyses because their isotopic values were not strongly divergent from those with C : N ratios < 4.0.

Dried plant samples were homogenized, and 5.0-mg samples were weighed into tin boats and analysed at the UCSC-SIL. Stable-isotope compositions for all sample types (gecko, arthropod, plant) are reported using the δ notation and referenced to Vienna PeeDee Belemnite for carbon and air for nitrogen.

Isotopic trophic discrimination factors and modelling approach

Extracting ecologically interesting and useful information from large isotopic data sets requires a series of decisions about how to organize the data and select appropriate trophic discrimination factors (Gannes *et al.* 1997; Moore & Semmens 2008). We have attempted to articulate our logic about potential sources of isotopic error (Table S3) and to account for that uncertainty in our assessments of food-web structure. Our strategy involved iteratively modelling diet for individual predators using a range of isotopic trophic discrimination factors in conjunction with a commonly used isotopic mixing model that explicitly incorporates source and mixture error. The result of this process is a set of distributions of possible diet compositions within each predator guild.

We analysed and compared isotopic values of protienaceous tissues only (e.g., keratin, muscle, cuticle), and thus

avoided complications that arise from differential routing of dietary macromolecules among different tissue types (Ambrose & Norr 1993). In general, the C and N in proteinaceous tissues of consumers with protein-rich diets (e.g., predators) are derived from the protein fraction of the diet (DeNiro & Epstein 1978, 1981). Keratin is an inert tissue, and the gecko scales we analysed likely formed over several months of animal growth and scale replacement. In contrast, muscle and cuticle are metabolically active and turn over on the order of weeks in locusts and spiders (Webb *et al.* 1997; Gratton & Forbes 2006). While diet is the primary control on the isotopic composition of the tissues we analysed, various physiological and life-history factors can also influence the isotopic composition of animal tissues (Gannes *et al.* 1997). We acknowledge these potential sources of error, but we believe that the population-level ecological patterns that we describe are broad enough to outweigh the individual-level isotopic effects of these other factors.

Before we compared consumer-tissue $\delta^{13}C$ and $\delta^{15}N$ values to the values of their diet sources, we accounted for preferential assimilation and excretion of diet-derived ^{13}C and ^{15}N. Isotopic differences between consumer tissue and diet are known as isotopic trophic discrimination factors (hereafter $\Delta^{13}C$ and $\Delta^{15}N$). $\Delta^{13}C$ and $\Delta^{15}N$ have not been experimentally defined for the specific taxa and tissues used in our study. We therefore relied upon general patterns of isotopic change between protein-rich tissues of primary and secondary consumers to define appropriate ranges of $\Delta^{13}C_{predator–prey}$ and $\Delta^{15}N_{predator–prey}$ values between both gecko β-keratin and predatory-arthropod protein on the one hand, and herbivore/detritivore (i.e. prey) protein on the other. We used three plausible $\Delta^{15}N_{predator–prey}$ values (1.5, 2.5 and 3.5‰) to reconstruct predator–prey trophic linkages (Oelbermann & Scheu 2002; Post 2002; McCutchan *et al.* 2003; Seminoff *et al.* 2007). We then assessed whether our interpretations were robust to this range of possible $\Delta^{15}N_{predator–prey}$ values. Likewise, to trace energy flow between the arboreal and terrestrial (i.e. C_3 vs. C_4) microhabitats, we applied a range of $\Delta^{13}C_{predator–prey}$ values (0.5, 1.5 and 2.5‰) to the predator $\delta^{13}C$ values to enable direct comparison with the prey $\delta^{13}C$ values (Oelbermann & Scheu 2002; Gratton & Forbes 2006; Seminoff *et al.* 2007). We did not attempt to compare directly the isotopic values of prey and vegetation.

To quantify the relative contributions of arboreal and terrestrial prey to predator diets, we used *IsoError 1.04* (Phillips & Gregg 2001), a stable-isotope mixing model that accounts for the variance in source (prey) and mixture (predator) isotopic values. Dietary mixing models are used to calculate the relative contributions of different sources to a consumer's diet. Much of the variation in the isotopic values of consumers is due to trophic position (reflected in $\delta^{15}N$ values) and the differing photosynthetic pathways of the two dominant plant types in the area (C_3 *Acacia* and C_4 grasses, reflected in $\delta^{13}C$ values; see Results for statistical tests). Once we accounted for the effect of trophic position on consumer $\delta^{15}N$ values, the remaining within-trophic-level variance in $\delta^{15}N$ values was not useful for determining energy flow between arboreal and terrestrial habitats. Therefore, we modelled the diets of geckos and predatory arthropods using a single-isotope ($\delta^{13}C$), two-source (arboreal and terrestrial prey) version of the mixing model. *IsoError* inputs for the diet sources (prey) and the mixture (predator) include $\delta^{13}C$ mean values, standard deviations, and sample sizes. We used the same two dietary sources (terrestrial and arboreal prey) for both sets of predators. We ran the *IsoError* model three times (with each of the three $\Delta^{13}C_{predator–prey}$ values listed above) for each individual predator, using replicate-sample (process) $\delta^{13}C$ error (SD = 0.5‰, equivalent for geckos and arthropods) as the predator error. We estimated the mean contribution of arboreal (C_3) prey to the diet of each individual predator, and then we compared the distributions of values for the different predator groups to examine differences in prey utilization.

Statistical analyses

Quantitative analyses were preformed using JMP 5.1 (SAS Institute, Cary, NC, USA). We assessed data visually for departures from normality. For normally distributed data, we used univariate and multivariate analyses of variance (MANOVA) to test for differences in $\delta^{13}C$ and $\delta^{15}N$ among groups. Following a significant MANOVA (according to Pillai's Trace test), we performed univariate contrasts with sequential Bonferroni corrections of α. For tests that involved non-normal data, we applied nonparametric MANOVA (npMANOVA: Anderson 2001) using PAST 1.81 (http://folk.uio.no/ohammer/past/), followed by nonparametric rank-sums tests.

RESULTS

Within-trophic-level differences

The raw $\delta^{13}C$ and $\delta^{15}N$ values of consumers exhibited a distinctive arch-shaped pattern, with prey in the two habitats most distinct in $\delta^{13}C$ values, and predators in both habitats showing less distinct isotopic values. Low variability of $\delta^{13}C$ within taxa suggested that identification to order or family provided sufficient taxonomic resolution to characterize major ecological patterns (Fig. 1, Table 1).

Arboreal and terrestrial prey had widely divergent isotopic values (Table 1; npMANOVA, $F_{2,69} = 44.8$, $P < 0.0001$), with the difference driven primarily by lower $\delta^{13}C$ values among

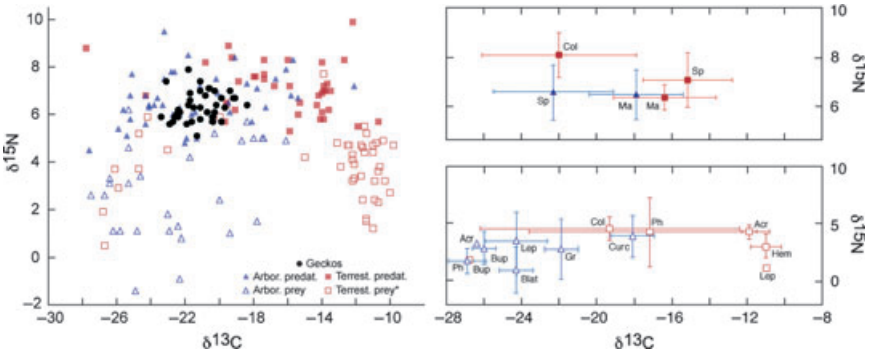

Figure 1 Left panel: scatterplot showing raw (i.e. not including isotopic trophic discrimination factors) values of $\delta^{13}C$ and $\delta^{15}N$ for each individual animal sampled for this study. Arbor., arboreal; Terrest., terrestrial; Predat., predator. The terrestrial prey category includes nine individuals (21%) with $\delta^{13}C$ signatures indicative of a C_3-plant-based diet, which might have fed on *Acacia*. Right panels: means (± SD) of arthropod raw $\delta^{13}C$ and $\delta^{15}N$ values by taxonomic affiliation for predators (top panel) and prey (bottom panel). Taxonomic abbreviations: Acr, Orthoptera, Acrididae (n = 1 arboreal and 11 terrestrial); Blat, Blattodea (n = 4); Bup, Coleoptera, Buprestidae (n = 4 arboreal and 1 terrestrial); Curc, Coleoptera, Curculionidae (*Myllocerus* sp., n = 9); Col, Coleoptera, other (n = 5 predators, and 11 terrestrial prey); Gr, Orthoptera, Gryllidae (n = 6); Hem, Hemiptera (n = 14); Lep, Lepidoptera (n = 3 arboreal and 1 terrestrial); Ma, Mantodea (n = 9 arboreal and 8 terrestrial); Ph, Phasmatodea (n = 2 arboreal and 4 terrestrial); Sp, spiders (n = 35 arboreal and 25 terrestrial).

Table 1 Summary statistics for the isotopic data set

Trophic grouping	N	Mean $\delta^{13}C$	SD $\delta^{13}C$	Mean $\delta^{15}N$	SD $\delta^{15}N$
Gecko	37	−21.2	1.2	6.3	0.6
Arboreal predator	44	−21.4	3.4	6.6	1.1
Terrestrial predator	38	−16.3	3.5	7.1	1.1
Arboreal prey	29	−22.4	3.4	2.9	2.1
Terrestrial prey	43	−14.3	5.6	3.9	1.4
C_3 tree	20	−28.4	0.3	1.4	1.0
C_4 grass	20	−12.3	0.2	2.2	0.7

tree- vs. grass-feeders (Wilcoxon $Z_{29,43} = -5.1$, $P < 0.0001$), and not by differences in $\delta^{15}N$ values (Wilcoxon $Z_{29,43} = -1.6$, $P = 0.10$). Arboreal and terrestrial arthropod predators and geckos were also significantly different (Table 1; npMANOVA, exact $F_{4,232} = 24.5$, $P < 0.0001$); pairwise contrasts revealed that geckos and arboreal predatory arthropods were indistinguishable ($P = 0.41$), and that both of these groups were isotopically distinct from terrestrial predatory arthropods ($P < 0.0001$). This difference appeared to be driven both by $\delta^{13}C$ values (Kruskal–Wallis, $\chi^2_2 = 45.4$, $P < 0.0001$) and by $\delta^{15}N$ values (ANOVA, $F_{2,116} = 6.1$, $P = 0.003$).

The $\delta^{13}C$ and $\delta^{15}N$ distributions of *Acacia* and grasses did not overlap (MANOVA, exact $F_{2,37} = 17934$, $P \ll 0.0001$; Fig. 2), reflecting the large photosynthesis-driven difference in $\delta^{13}C$ values between plant types (ANOVA, $F_{1,38} = 36783$, $P \ll 0.0001$). $\delta^{15}N$ values of the two plant groups also showed substantial (though less dramatic) differences: *Acacia* $\delta^{15}N$ values were significantly lower than grass $\delta^{15}N$ values, (ANOVA, $F_{1,38} = 7.9$, $P = 0.008$), which is expected because *Acacia* are leguminous N_2-fixing plants, and grasses are not (Högberg 1997).

Among-trophic-level differences

To illuminate predator–prey relationships, we applied $\Delta^{15}N_{predator-prey}$ values to predator $\delta^{15}N$ values and then evaluated the extent of overlap between these values and those of their presumed prey (arboreal and terrestrial arthropods were combined here for a habitat-independent comparison). Arthropod predator and prey $\delta^{15}N$ distributions overlapped using one of the three $\Delta^{15}N_{predator-prey}$ values (3.5‰), but predator $\delta^{15}N$ values were higher when $\Delta^{15}N_{predator-prey} = 1.5‰$ (ANOVA, $F_{1,152} = 63.8$, $P < 0.0001$) and 2.5‰ (ANOVA, $F_{1,152} = 13.4$, $P = 0.0003$). Gecko and prey $\delta^{15}N$ distributions overlapped with $\Delta^{15}N_{predator-prey} = 2.5‰$, but not with 1.5‰ ($F_{1,107} = 5.0$, $P = 0.03$) or 3.5‰ ($F_{1,107} = 20.6$, $P < 0.0001$; Fig. 2 shows these relationships using the intermediate $\Delta^{15}N_{predator-prey} = 2.5‰$).

From these analyses, it appears that both geckos and predatory arthropods may derive some of their diet from intraguild prey. That said, there is clearly much variation in $\delta^{15}N$ values at all trophic levels in this system. The distribution in prey $\delta^{15}N$ values alone accounts for between two and four trophic 'steps' (using $\Delta^{15}N_{predator-prey} = 3.5‰$ and 1.5‰, respectively); thus, a large portion of the range in predator $\delta^{15}N$ values may simply reflect the broad range in prey $\delta^{15}N$ values. The inferred extent of intraguild predation depends heavily on $\Delta^{15}N_{predator-prey}$ and therefore cannot be quantified, as we do not know $\Delta^{15}N_{predator-prey}$ values with certainty. These $\delta^{15}N$ results helped to inform our selection

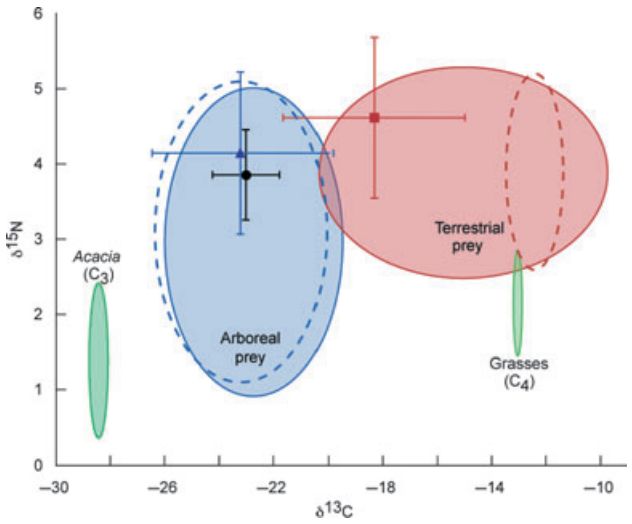

Figure 2 Dietary reconstruction for predatory animals (arboreal arthropods, terrestrial arthropods, geckos; symbols as in Fig. 1). Isotopic values for plants and prey are represented by ellipses spanning ± 1 SD on both axes. The solid, shaded ellipses represent values obtained when all terrestrial C_3-feeding prey are treated as ground-dwelling forb specialists; the dashed, open ellipses represent values obtained when all terrestrial C_3-feeding prey are treated as displaced *Acacia* feeders. The true scenario likely falls between these two extremes. Predator $\delta^{13}C$ and $\delta^{15}N$ values are plotted as the observed value + the intermediate trophic discrimination factors (−1.5‰ for $\delta^{13}C$ and −2.5‰ for $\delta^{15}N$), so that the resulting means and distributions are shown as the values of their presumed prey. Error bars represent ± 1 SD.

of a broad range of $\Delta^{13}C_{predator–prey}$ values that account for the possibility of intraguild predation.

Predator diets

We compared the distributions of mean proportions of C_3 prey among the nine possible combinations of predator types (arboreal arthropod, terrestrial arthropod, gecko) and $\Delta^{13}C_{predator–prey}$ values (0.5, 1.5 and 2.5‰). We used a wide range in $\Delta^{13}C_{predator–prey}$ values to account for the potential additive effects of intraguild predation on *IsoError* modelling. Proportions of C_3-derived diet differed significantly among groups (Kruskal–Wallis, $\chi^2_2 = 53.6$, $P < 0.0001$); post-hoc comparisons revealed a sharp split between arboreal and terrestrial predator groups, with no differences among predator groups *within* either of these two habitat types ($\chi^2_1 = 0.2$, $P = 0.7$). The patterns of C_3-resource use among predator groups were robust to individual-level error associated with *IsoError* modelling; the standard error of the mean proportion of C_3-derived diet for an individual predator ranged from 0.08 to 0.19.

The calculated contributions of C_3 prey to predator diets varied somewhat depending upon the $\Delta^{13}C_{predator–prey}$ value used during the *IsoError* model runs. For geckos, the proportions ranged from 0.89 ± 0.12 ($\Delta^{13}C_{predator–prey}$ = 0.5‰) to 0.99 ± 0.04 ($\Delta^{13}C_{predator–prey}$ = 2.5‰); for arboreal predatory arthropods, from 0.81 ± 0.29 ($\Delta^{13}C_{predator–prey}$ = 0.5‰) to 0.89 ± 0.21 ($\Delta^{13}C_{predator–prey}$ = 2.5‰); and for terrestrial predatory arthropods, from 0.31 ± 0.33 ($\Delta^{13}C_{predator–prey}$ = 0.5‰) to 0.52 ± 0.33 ($\Delta^{13}C_{predator–prey}$ = 2.5‰).

We tested for seasonal differences (wet vs. dry) in the $\delta^{13}C$ values of the three taxonomic groups with sufficient sample sizes: terrestrial spiders, arboreal spiders, and geckos. The distributions of wet and dry season terrestrial spider $\delta^{13}C$ values were indistinguishable (ANOVA; $F_{1,23} = 1.1$, $P = 0.31$), suggesting that terrestrial predators link the two food subwebs regardless of season. The $\delta^{13}C$ values of both arboreal spiders and geckos were lower (by 3.5‰ and 1.3‰, respectively) during the dry season, suggesting that arboreal predators may have stronger fidelity to trees during drier conditions. Overall, the data show relative specialization of tree-dwelling predators upon tree-feeding prey, with ground-dwelling predators drawing considerable proportions of their diet from both C_3- and C_4-based sources (Fig. 3).

DISCUSSION

Our savanna system can be conceptualized as consisting of two habitats (arboreal and terrestrial) and comprising two distinct energy-assimilation pathways (C_3 and C_4 photosynthesis). The 'boundary' between these two habitats is vertical space. Our data indicate relatively strong specialization of herbivores on either C_3 or C_4 plants, and of tree-dwelling predators (especially spiders and geckos) upon tree-feeding prey. In contrast, regardless of the assumptions used to model the data, ground-dwelling predators derived a considerable proportion of their diet from prey feeding on both C_3 and C_4 resources.

In our view, the most parsimonious explanation for these results is that things fall down. In other words, specialized C_3-feeding insects (with the exception of the curculionid beetle *Myllocerus* sp., which exhibited intermediate $\delta^{13}C$ values: Fig. 1) tend to be passively transported by gravity to the ground, where they not infrequently fall victim to a set of largely opportunistic terrestrial predators. Tree-dwelling predators (especially spiders and geckos), to the extent that they also tend to fall down, do not stay on the ground long enough to forage, but instead resume positions in arboreal microhabitats. (Personal observations support this supposition: geckos rapidly return to trees if dropped or chased off.) Of the arboreal predators, only a few mantids appeared to derive appreciable energy from C_4-feeding prey (Fig. 1). If

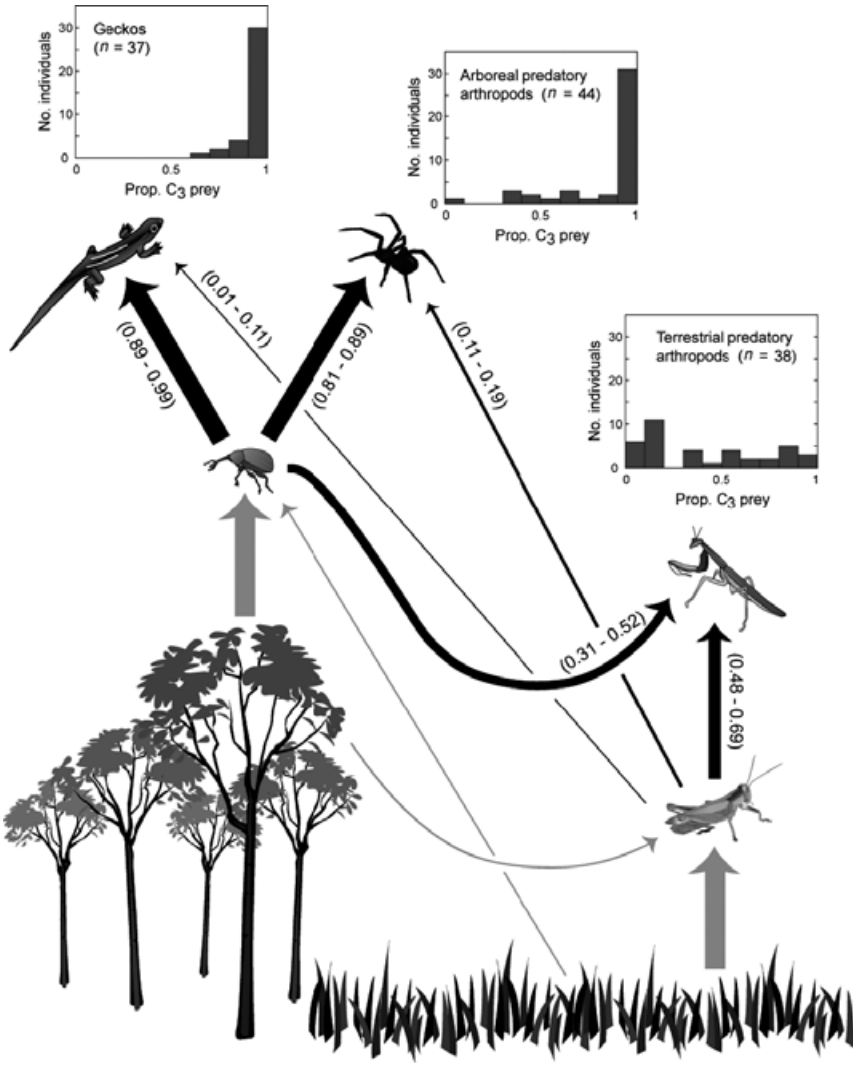

Figure 3 Schematic diagram of the trophic linkages investigated in this study. Values in parentheses give the range of three mean dietary proportions of C_3-feeding prey for each link, calculated using *IsoError* with $\delta^{13}C$ trophic discrimination factors ($\Delta^{13}C$) of 0.5‰, 1.5‰, and 2.5‰. Links between predators and prey (black lines) are proportional in width to the mean proportion of diet constituted by that link, obtained using the intermediate $\Delta^{13}C$ = 1.5‰. Histograms illustrate the proportion of C_3-feeding prey in the diets of individual predators, also obtained with $\Delta^{13}C$ = 1.5‰. The width of the links between prey and plants (grey lines) reflect estimated, not calculated, diet proportions.

not quite a one-way energetic street from trees to grass, it is a street with at least three lanes in that direction and one in the other (Fig. 3).

Several facts support this interpretation. First, we found nine apparent C_3-specialist prey items within the grass (*c.* 21%; Fig. 1), but no C_4 specialists in trees. While it is possible that some of the C_3-feeding individuals in our terrestrial samples were forb specialists, the relative cover of non-grasses in the herbaceous layer (*c.* 3%, and as low as 1–2% in some years: Riginos & Grace 2008; T. P. Young, unpublished data) seems too low to account for the *c.* 40% of terrestrial predator diet derived from C_3 sources. Finally, while it is also possible that some terrestrial predators are more mobile than most arboreal ones, many clearly are not. The spiders collected from both trees and grasses contained a mixture of sit-and-wait and actively foraging species; moreover, several recent studies have emphasized that ground-dwelling spider guilds partition microhabitat into relatively narrow 'habitat domains,' with even relatively active species utilizing only a subset of the herbaceous plant layer (Schmitz 2005, 2007; Preisser *et al.* 2007). Even if ground-dwelling predators *were* more mobile and

behaviourally labile, able to forage in both grass and tree canopies, this would still reflect intriguing functional non-equivalence among predator groups in terms of coupling energy channels.

Prey subsidies of this type are not uncommon. Several studies document cases of insects dropping from trees into water, where they are eaten by fish (Mason & MacDonald 1982; Nakano & Murakami 2001; Baxter *et al.* 2004), and the role of gravity is implicit in discussions of benthic-pelagic coupling and of watersheds feeding streams. There are likewise multiple examples of subsidies travelling against gravity, as when emerging aquatic insects subsidize riparian zones (Nakano & Murakami 2001; Power *et al.* 2004). But we are not aware of any studies quantifying subsidies from tree canopies to the herbaceous layer within wooded ecosystems. This may be because we conceive of most habitat boundaries as occurring in horizontal, rather than vertical, space. In other words, most ecologists would agree that a shoreline or forest edge constitutes a habitat boundary, whereas the trees and grasses in our system are typically considered part of the same savanna habitat. That formulation may obscure important processes in systems like ours, where arboreal and terrestrial animal communities comprise a largely non-overlapping set of species deriving energy from distinct sources (C_3-photosynthesizing, N_2-fixing trees and C_4-photosynthesizing, non-fixing grasses). According to this view, most published examples of cross-ecosystem subsidies represent dramatic, large-scale, manifestations of a ubiquitous structuring process that operates on multiple scales.

At a more conceptual level, several recent studies have explored the role of predators in linking food webs from different habitats, and the stabilizing effects conferred by such linkage (Post *et al.* 2000; McCann *et al.* 2005; Rooney *et al.* 2006). A linchpin of these models is that the consumers at each successive trophic level tend to be more mobile than their prey, which allows top predators to integrate energy channels originating in multiple habitats. Our results reconfirm the role of predators in coupling consumer-resource chains from different habitats (note the similarity between our Fig. 1 and that of Rooney *et al.* (2006), both of which illustrate that predators derive carbon from two distinct sources), but with a qualification. In the present case, predators are not necessarily mobile, but rather are of habitat-specific types. An abiotic conveyor (gravity) drives a prey subsidy in one direction (down), with the result that the predators in each habitat are functionally non-equivalent: one type (terrestrial) is a stronger 'channel coupler' than the other. This finding is illustrated in Figs. 1 and 2, where terrestrial predators span a range of $\delta^{13}C$ that is intermediate between the respective ranges of terrestrial and arboreal prey.

Thus, the role of predators in linking food chains, and hence stabilizing ecosystems, may be even more general than indicated by these earlier studies. Where consistent subsidies occur, predator mobility is not required: even sessile terrestrial carnivores such as pitcher plants and myrmeleontid larvae can theoretically fill this functional role. Moreover, we suggest that abiotic physical conveyors such as gravity, wind, and currents may be less sensitive to perturbation (e.g., anthropogenic landscape change) than mechanisms that hinge on unrestrained movement by consumers.

We offer two caveats to our interpretation of these data. First, falling detritus is central to ecosystem ecology (Vitousek 1984), suggesting that detritivores should also effectively couple energy channels in this and other vertically structured systems. Second, a falling-prey subsidy in no way excludes the possibility that high predator mobility *also* functions to couple distinct energy channels in our system. For example, higher mobility of mantids relative to spiders might explain why $\delta^{13}C$ values of arboreal and terrestrial mantids were not as distinct as those of spiders from the two habitats (Fig. 1).

Because food-web stability is enhanced by the coupling of multiple energy channels (Rooney *et al.* 2006), the relative abundance of C_3 and C_4 plants in savannas might be a strong determinant of food-web structure and dynamics. The obvious way to test the importance of the arboreal prey subsidy to the terrestrial community is to cut off the subsidy and monitor the responses of terrestrial arthropod and plant communities. Because *Acacia* is a relatively high-quality resource relative to grass (30% higher N content; KFD, unpublished data), falling prey may elevate ground-dwelling predator populations above levels attainable with an exclusive reliance on *in situ* C_4-feeding prey (Polis *et al.* 1997). In this case, subsidy elimination might suppress ground-dwelling predator populations (Sabo & Power 2002), potentially releasing terrestrial herbivore populations from top-down control and decreasing grass cover (Holt 1977; Polis & Hurd 1996). Along these lines, Murakami & Nakano (2002) have shown that riparian birds subsidized by emergent aquatic insects depress terrestrial leaf rollers to a greater extent than unsubsidized birds in upland forest. It would also be helpful to know how the importance of the falling-prey subsidy varies as a function of distance from nearby trees. Finally, predators are known to increase rates of jumping or falling by prey (Haemig 1997; Losey & Denno 1998). In our system, *Acacia* ants (*Crematogaster* spp.) may similarly enhance rates of prey rain, indirectly promoting the linkage of the C_3- and C_4-based food webs.

When applied conservatively, stable isotope techniques are an effective way to identify and quantify energy and nutrient flow within and among food webs. Yet most natural-abundance isotopic studies of spatial subsidies have relied upon the relatively strong isotopic gradients that can exist between freshwater, marine, and terrestrial ecosystems ($\delta^{13}C$ and $\delta^{15}N$ values, e.g., Akamatsu *et al.* 2004; Barrett

et al. 2005), or between C_3 and C_4 terrestrial plants ($\delta^{13}C$ values, e.g., Magnusson *et al.* 2001, this study). Our results illustrate the importance of vertical habitat structure in determining to food-web form and function in a wooded grassland, but falling-prey subsidies are likely an important part of trophic dynamics in forests worldwide. Such vertical energy transfer will be difficult to investigate isotopically in forested ecosystems where C_4 plants are not abundant. Innovative isotopic techniques, perhaps using other stable-isotope systems (δ^2H, $\delta^{18}O$) or isotopic-enrichment experiments, may inform the study of food-web connectivity among a wider range of terrestrial habitats and microhabitats.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Table S1 List of animal samples.
Table S2 List of plant samples.
Table S3 Isotopic error and assumptions.

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