AN UNUSUAL TROPHIC SUBSIDY AND SPECIES DOMINANCE IN A TROPICAL STREAM

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Abstract. In classical theory, species are assumed to achieve dominance through competitive exclusion, but if food resources are limiting, cross-habitat trophic subsidies could also underpin dominance. The impact of dominant species on community dynamics may depend on the energy base of population size. We report on an unusual, spatially subsidized population of a tropical, stream-dwelling crab that dominates the benthic fauna of a Kenyan stream. Diet and stable isotope analyses indicated that this crab is a true omnivore, with terrestrial subsidies dominating both plant and animal resources. Unusually, the animal prey included almost no aquatic invertebrates. Instead, a single species of ant constituted ~35% of the annual diet (stomach contents analysis) and up to 90% of assimilated nitrogen (estimates from stable isotope analysis). Ants may be pivotal to enabling crab dominance, and this crab may be largely disconnected from the local trophic network for its dietary needs. The paucity of other invertebrates in the stream community suggests that this super-dominant crab is a strong interactor that suppresses aquatic invertebrate populations. Common stabilizing attributes of spatially subsidized food webs (e.g., asynchronous prey availability, wide feeding niche, consumer migration) were absent from this system, and although apparently stable, it may be vulnerable to disturbance in the donor habitat.

Key words: diet; East Africa; freshwater crabs; mixing model; Potamonautes; *spatial subsidy; stable isotopes; stomach contents.*

Introduction

Patterns in the relative abundance of species and the processes producing those patterns underpin our understanding of biological diversity and species coexistence (Tokeshi 1999). Rare species are of particular interest in the context of biological conservation (e.g., Gaston 1994), but common or dominant species can be the main drivers of community structure and ecosystem processes (Smith and Knapp 2003, Dangles and Malmqvist 2004). Thus, understanding the manner in which species dominance is achieved and maintained is key to many aspects of community and ecosystem ecology. In classical ecological theory, species are usually assumed to achieve dominance through competitive exclusion, i.e., to exploit a disproportionate share of in situ resources. Alternatively, if food is a limiting resource, cross-habitat trophic subsidies may decouple local consumer–resource dynamics, resulting in populations much larger than possible on in situ resources alone

(Polis et al. 1997). Dominant species that are underpinned by spatial subsidies may have extra strong impacts on local communities, i.e., they become superdominants. Spatially subsidized food webs have been documented for many systems and include movement of nutrients, detritus, prey, and consumers among habitats (e.g., articles and references in Polis et al. 1997, 2004), but it is unclear how or whether subsidies can alter the role of dominant species.

Does the role of a super-dominant species in the trophic network differ from that of a dominant species that relies on in situ resources? As a consumer, a super-dominant species could derive significant nutritional benefit from both ex situ and in situ resources (Fig. 1a), or it could be strongly dependent on ex situ resources and largely "disconnected" from the local trophic network for its dietary needs (Fig. 1b). What impact does a super-dominant have on its resources? Spatial subsidies rarely involve recipient control so ex situ resources are likely to be unaffected by the consumer (Fig. 2). Within the main habitat, however, the super-dominant may be a strong interactor with high impacts on in situ resource abundance and community dynamics (Fig. 2a). This is largely a magnification of the traditional top-down role played by dominant consumers in trophic networks and is likely to occur where significant nutritional benefit is derived in situ (Fig. 1a).
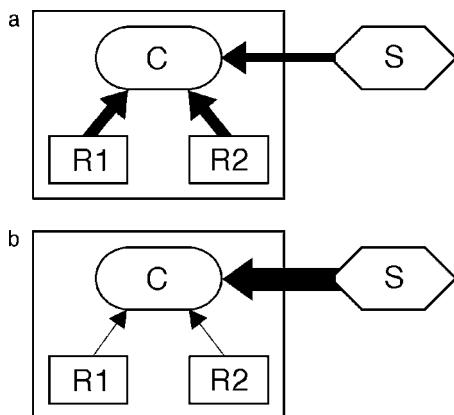
FIG. 1. Two trophic networks illustrating the relative dietary importance of different resources to a super-dominant consumer (C). R1 and R2 are in situ resources; S is an ex situ trophic subsidy. (a) The consumer derives significant benefit from both in and ex situ resources. (b) The consumer derives significant benefit from ex situ resources but is largely disconnected from in situ resources for dietary needs. Arrow width reflects the relative magnitude of dietary contribution.

If a super-dominant is nutritionally disconnected from the local trophic network and in situ resources are abundant, then weak interactions with the local community are likely (Fig. 2b). Here, the consumer population is under direct donor control and community dynamics within the main habitat may differ markedly from those in Fig. 2a. If in situ resources are scarce, a disconnected super-dominant may still be a strong interactor, through diffuse consumption across a large consumer population (see *Discussion*) or through more complex processes involving, for example, behavioral interactions (cf. behaviorally mediated trophic cascades; Schmitz et al. 1997, Fortin et al. 2005).

This study focuses on a stream system, and subsidies between terrestrial and running waters are well documented. Subsidies of detritus from terrestrial vegetation are common and often energetically important (e.g., Wallace et al. 1999). Subsidies of animal prey typically involve a rain of terrestrial invertebrates that are consumed mainly by fishes, and often a reciprocal flux of adult aquatic insects into the riparian zone, where they are consumed by diverse terrestrial predators (for a review see Baxter et al. 2005). Predator densities in both habitats may be increased as a result of these prey subsidies (Nakano and Murakami 2001), and the effects of interrupting these subsidies can cascade through both ecosystems (Baxter et al. 2004).

Freshwater crabs often dominate the benthic fauna of tropical streams and may play a key role in ecosystem processes, such as detritus processing (Dobson et al. 2002). They can have very high density and biomass (≥ 5 g/m^2 dry mass), often comprising >70% of the total macroinvertebrate biomass (Dobson et al. 2007a, b). Crab dominance may be associated with particular life-history patterns (Dobson et al. 2007a), but we lack an

understanding of the resource/energy base and the consequences for ecosystem processes. The general species abundance pattern, however, is characteristic of top-down effects in spatially subsidized food webs, in which a food subsidy allows the consumer to maintain high biomass, with consequent suppression of the consumer's in situ resources (Polis and Strong 1996, Polis et al. 1997).

Lotic crabs appear to be true omnivores (sensu Coll and Guershon 2002), with a diet dominated by detritus and a lesser proportion of freshwater invertebrates (Williams 1962, 1965, Hill and O'Keefe 1992), although comprehensive diet studies are scarce. High biomass for omnivorous crabs and crayfish in streams may be possible only if animal prey are a large part of the diet (Momot 1995), and, indeed, many marine and freshwater crabs grow and reproduce better on a diet that includes animal prey than a purely detritivorous or herbivorous diet (Kennish 1997, Wen et al. 2002, Buck et al. 2003). This may be related to the relatively low nitrogen content of plant material and low nitrogen uptake by these decapods, coupled with the constraints of gut volume and gut clearance rate (Wolcott and Wolcott 1984, 1987). Thus, if the dominance of freshwater crabs is facilitated by a cross-habitat food subsidy, then it is likely to be a direct subsidy of animal prey rather than detritus.

Here we report on the feeding habits of a tropical, stream-dwelling crab whose density and biomass estimates in a Kenyan stream are considered high for freshwater invertebrates (Dobson et al. 2007a), yet which inhabits a stream where the density of other macroinvertebrates is extraordinarily low. Our objective was to determine the energetic basis of crab dominance
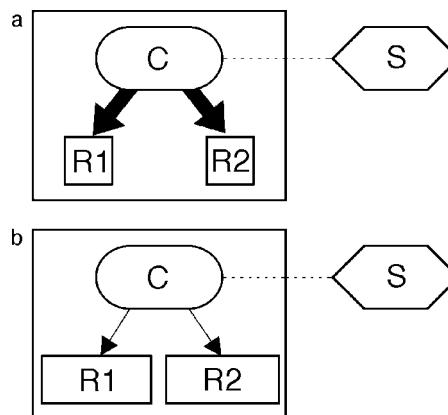

FIG. 2. Two interaction networks illustrating the relative impact of a super-dominant consumer on its resources. Abbreviations as in Fig. 1. The consumer has (a) a strong impact on in situ resources, which, consequently, are low in abundance or (b) a weak impact on in situ resources, which subsequently are abundant. The consumer has no impact on ex situ resources, i.e., no recipient control. Arrow width reflects the relative magnitude of consumer impact; box sizes of R1 and R2 reflect their relative abundance.

and to test whether cross-habitat subsidies (Polis et al. 1997) might contribute to population size, i.e., which, if any, of the scenarios in Fig. 1 is applicable? We examined crab diet through stomach contents analysis and stable isotope analyses. Dual- and single-isotope mixing models were used to estimate the relative contribution of the major food resources to crab nutrition and to determine whether carbon and nitrogen consumption is decoupled in this omnivore (e.g., Stenroth et al. 2006). If this crab is a super-dominant, the next step is to assess its impact on the local community (e.g., Fig. 2). Diet studies cannot provide definitive tests of interaction strength, but we use our survey data to gain insight into the predatory role this crab may play.

METHODS

Study site and species

Our study species, a small-bodied crab in the genus *Potamonautes* (Decapoda: Potamonautidae), is new to science and awaits formal description (N. Cumberlidge, *personal communication*) and is referred to here as the Chinga crab. The life history of this species is described by Dobson et al. (2007a) and, at the study site in Kenya, population density and biomass remain constant throughout the year, reproduction occurs year-round with no clear breeding season, and consequently, the population size structure also remains constant. Crabs dominate the stream community in terms of density and biomass: 24.8 individuals/m^2 and 4.6 g/m^2 (Dobson et al. 2007a). The density of other macroinvertebrates is extraordinarily low (<150 individuals/m^2; Gachoki 2005) and <10% of densities in other Kenyan streams (Dobson et al. 2002).

The study was carried out in the headwaters of the Chinga River (0°0′15.84″ N, 36°15′33.12″ E, altitude 2180 m), a small tributary of the Subukia River draining the eastern slope of the Kenyan Rift Valley. Upstream of the study site, the river descends the Rift Valley wall as a series of waterfalls in thick forest; the study site itself runs through a strip of remnant montane forest across a shallow gradient. The channel averages 1 m wide and is typically <10 cm deep during normal flow; it is fed by several small springs, whose outflow channels are ~0.5 m wide. Riparian vegetation is dominated by large trees, particularly *Syzygium cordatum* and *Ficus* sp. The stream was heavily shaded and consequently there was little algal growth. The substrate is loose cobble, with numerous aggregations of detritus associated with trailing vegetation and tree roots. There were no macrophytes, and fish appeared to be absent from the stream. The climate of the Chinga River is largely aseasonal, with little variation in temperature. The area is subject to seasonal rainfall, with heavier rains in March–May and lighter rains from July to December. Rain can, however, fall at any time of year. Although stream discharge varies seasonally and in synchrony with rainfall, wet and dry seasons are weakly defined.

More detailed site information and climatic and physicochemical data are reported in Dobson et al. (2007a).

Sample collection and diet analyses

Crabs for diet analysis were collected approximately every two months for just over one year (March 2004–May 2005). Between 20 and 32 crabs were collected on each occasion, with an attempt to collect equal numbers of males and females, juveniles and adults. Crabs were collected from the main channel and from spring outflows; they were preserved and stored in methylated spirit and, before dissection, carapace width was measured with calipers. The contents of each crab's cardiac stomach were removed by dissection and mounted on microscope slides using Euparal (Fisher Scientific UK, Loughborough, UK).

Foraging success of each individual was expressed as the ratio of measured stomach contents to maximum stomach fullness for a crab of that size. Microscope slides with stomach contents were digitized at 78 pixels/mm and analyzed using the public domain software ImageJ (Rasband 1997–2006). The area covered by all particles >0.01 mm^2 was calculated, and this provided an estimate of stomach fullness. The relationship between stomach fullness and crab size was characterized using quantile regression (see *Statistical and numerical analyses*), and the upper quantile equation was used as an estimate of maximum stomach fullness.

To estimate the relative abundance of different food items in the diet, a 1-mm grid was superimposed upon each microscope slide, and the presence/absence of various food types was recorded for each grid square. The relative abundance of each item was expressed as the number of grid squares containing that item, divided by the total number of squares containing any food particles. Grid squares containing two or more food items were weighted accordingly. For 90% of the crabs, the number of grid squares containing food items was >100, so estimates of the relative abundance of food items was accurate to <1% for most individuals.

For analyses of carbon and nitrogen stable isotopes, samples of crabs and their putative food resources were collected during dry (December 2005) and wet seasons (March 2006). In each season, we collected 15 crabs (five adult, five subadult, five juvenile), mixed detritus and identifiable leaves of common riparian plants from the river channel, representatives of the common aquatic macroinvertebrates and terrestrial ants (the taxon consumed by crabs). Detritus and leaves were air-dried; animals were frozen and then air-dried. Crabs were frozen initially, then muscles were dissected from the legs and claws of each individual and dried for stable isotope analysis. Other invertebrates were relatively small and whole bodies of multiple individuals were pooled to provide enough material for analysis. Dry material was homogenized with an antistatic mortar and pestle, loaded into tin capsules, and analyzed on a

continuous flow isotope ratio mass spectrometer at the Scottish Universities Environmental Research Centre (East Kilbride, UK). All stable isotope ratios are reported in per mil (‰) using the standard notation relative to international standards. Repeated analysis of laboratory standards showed precision (standard deviation) to be equal to, or better than, 0.30‰ for $\delta^{15}N$ and 0.14‰ for $\delta^{13}C$.

Statistical and numerical analyses

The relationship between stomach fullness and crab size was characterized as a limiting response using quantile regression (Cade and Noon 2003, Koenker 2005). Quantile regression extends classical regression (i.e., a single model for central tendency of a response, conditional on a predictor variable) to the full range of conditional quantile functions (i.e., a family of statistical models for the median and all other quantiles). The 95th quantile equation ($\tau = 0.95$) was used as an estimate of size-specific, maximum stomach fullness. Analyses were carried out using the quantreg package in R Project software (R Development Core Team 2004). To determine which model (e.g., linear, quadratic, exponential) of the 95th quantile better described the data, we used a tau-specific version of the Akaike Information Criterion (Cade et al. 2005: Appendix C), weighted for small sample size (Johnson and Omland 2004). Quantile regression ANOVA (within the quantreg package of R) was used to test whether model coefficients were significantly different between upper and lower quantiles ($\tau = 0.95$ and $\tau = 0.05$).

Effects of date, crab size, and sex on diet composition were tested using MANOVA, as some dietary elements were correlated. Foraging success was not correlated with diet composition, and the effects of the same independent variables were tested using ANOVA. Diet composition and foraging success were expressed as proportions and, hence, were arcsine square-root transformed to satisfy the assumptions of the statistical tests. The effects of season, crab age, and sex on stable isotope values were tested using ANOVA.

We used dual- and single-isotope, source-based mixing models to estimate the relative contribution of different food resources to crab muscle. Single isotope models can handle a maximum of two resources, x and y. The proportion of resource x assimilated by consumer a is expressed as

$$p_x = \frac{a_i - x_i - f_i}{x_i - y_i} \qquad (1)$$

where a_i, x_i, and y_i are the isotope values of element i for the consumer, resources x and y, respectively, and f_i is the fractionation expected between consumer and resource for element i. The proportion of the other food resource, p_y, is simply $1 - p_x$. Separate equations are used for each element, e.g., nitrogen and carbon. Dual-isotope models can determine the relative contribution of up to three different food sources (x, y, and z),

provided that isotope values are available for two elements, i and j. The mixing model is solved as a set of three simultaneous equations:

$$a_i = p_x(x_i + f_i) + p_y(y_i + f_i) + p_z(z_i + f_i) \qquad (2)$$

$$a_j = p_x(x_j + f_j) + p_y(y_j + f_j) + p_z(z_j + f_j) \qquad (3)$$

$$1 = p_x + p_y + p_z \qquad (4)$$

where p_x, p_y, and p_z are the proportions of prey resource items x, y, and z assimilated from the diet.

Dual-isotope models can be applied when there are two or three resources, but they also assume that equal proportions of carbon and nitrogen are assimilated from each food source. We did not know a priori whether this assumption is appropriate for the Chinga crab, but evidence suggests that C and N sources may be decoupled for omnivores, especially when food sources differ markedly in C:N (Stenroth et al. 2006). Single-isotope models involve fewer food sources, but do not assume equal proportions of C and N are assimilated from each source. Thus, by using both model types, we investigated whether C and N consumption might be decoupled.

Source-based mixing models require independent and species-specific information on fractionation values and, as no empirical values exist for the Chinga crab, we used literature-based values for muscle tissues of other freshwater decapods. In particular, Rudnick and Resh (2005) examined muscle tissues of the Chinese mitten crab, *Eriocheir sinensis* (Milne Edwards), and red swamp crayfish, *Procambarus clarkii* (Girard), reared on isotopically constant diets and reported carbon fractionation (f_C) values of ~2.0 for animals fed low and high C:N diets and nitrogen fractionation (f_N) of 1.0–2.9 on low C:N and 6.0 on high C:N diets. The C:N ratios of food sources can influence assimilation rates (e.g., Adams and Sterner 2000) so our mixing models used f_N values appropriate for the C:N value of each food source and explored the effect of uncertainty or variation in fractionation values on the model solutions and ecological interpretation. Thus, Eq. 1 was modified as

$$p_x = \frac{a_i - (x_i + f_{xi})}{(x_i + f_{xi}) - (y_i + f_{yi})} \qquad (5)$$

where f_{xi} and f_{yj} are resource-specific fractionation values. Similar modifications were made to the f_i values in the set of simultaneous equations (Eqs. 2–4) used in dual-isotope models. We imposed only the condition that f_N must be lower for low C:N foods than high C:N foods, and vice versa for f_C. Source-based mixing models assume that consumers are in isotopic equilibrium with their resources. No information is available regarding isotopic turnover rates in tissues of the Chinga crab, but the aseasonality in this species' population dynamics (Dobson et al. 2007a) and the absence of temporal or ontogenetic variation in crab diet or in the isotope
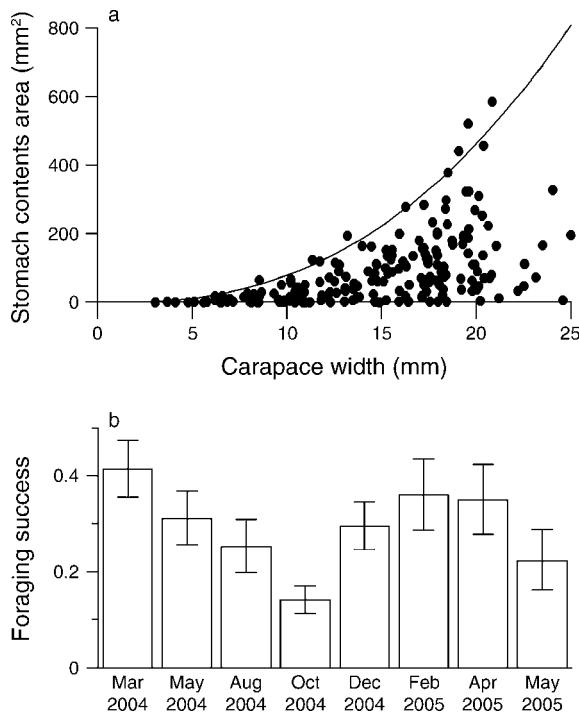
FIG. 3. (a) Foraging success based on the relationship between stomach fullness (estimated as area of particles in the stomach) and crab size (carapace width, CW), based on all Chinga crabs in all seasons. The solid line is the 95th quantile line, an estimate of maximum fullness possible: area $= -2.87 + 0.259 \times CW^{2.5}$; quantile regression ANOVA, $F_{1, 378} = 75.0$, $P < 0.001$. (b) Foraging success (mean $\pm$ SE) of crabs in each month (ANOVA testing effect of date on foraging success, $F_{7, 190} = 2.63$, $P = 0.013$).

values of crab muscle (see *Results*) suggest that our analyses are likely to be robust to this assumption.

RESULTS

Crab size limited maximum food consumption, but was unrelated to average consumption, i.e., stomach fullness varied with crab size, but crabs of any size could have empty or nearly empty stomachs (Fig. 3a). Preliminary analyses indicated that foraging success (stomach fullness/maximum stomach fullness) was not related to crab size or sex, and these variables were omitted from subsequent tests. Foraging success varied temporally (Fig. 3b), but was not obviously associated with seasonal cycles: values were lowest during the early dry season (October) and highest during the rainy season (March), but high values also occurred during part of the dry season (February) and low values in the wet (May 2005). Thus, temporal variation in foraging success requires cautious interpretation and foraging success may be driven by episodic events rather than seasonal cycles.

Terrestrial ants and detritus from the stream channel made up >90% of the diet, with an assortment of other invertebrates comprising the remainder (Fig. 4). These small-bodied ants (head width ~0.5 mm, total length

~2.5 mm) are in the genus *Pheidole* Westwood, subfamily Myrmicinae, and were almost certainly all one species, but species-level identification was not attempted as this is a large and taxonomically confused genus (Taylor 2006). The stomachs of larger crabs commonly contained 50–100 ants (>100 in some cases), and ants were the sole food items in the stomachs of ~25% of the crabs. Other invertebrates in the diet included a few freshwater taxa (mainly Ephemeroptera and Diptera), a diverse array of terrestrial taxa or fragments thereof, and the moulted skins of caterpillars. The range of invertebrate species in the diet was high but, other than ants, none was abundant. Observation of detrital particles suggested that either small particles (<2 mm^2) were collected from the channel or larger particles
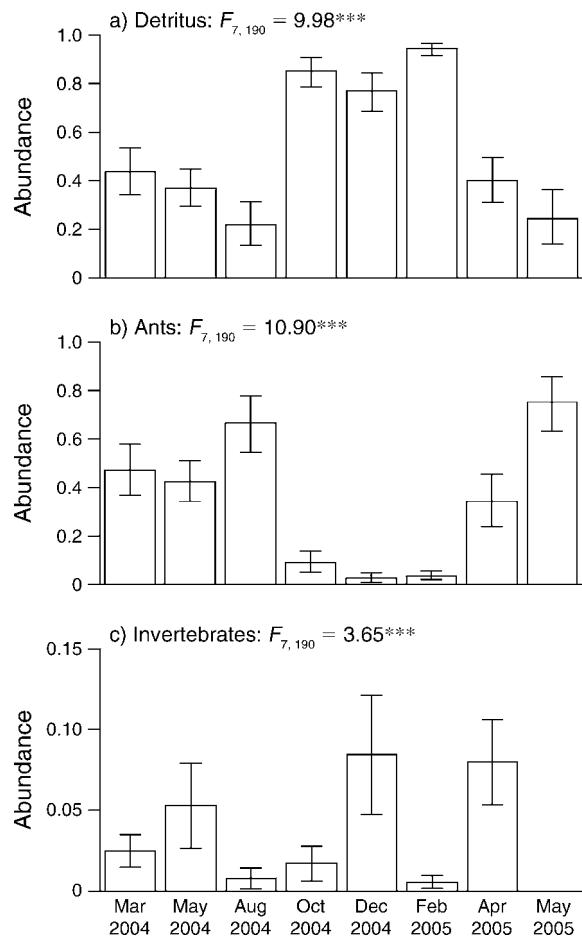

FIG. 4. Relative abundance (mean $\pm$ SE) of (a) detritus, (b) ants, and (c) invertebrates in Chinga crab diet in each month. Data are expressed as the proportional area of food items in stomach contents mounted on microscope slides. Note that the *y*-axis scale is much shorter in (c) than in (a) and (b). In (c), no crabs had non-ant invertebrates in their stomachs in May 2005. Means and SE were estimated from arcsine square-root-transformed data and back-transformed for graphical purposes. Statistics reported in each panel are univariate ANOVA after MANOVA involving all three food types (Wilks' $\lambda = 0.607$, $F_{21, 540} = 4.70$, $P < 0.001$).
*** $P < 0.001$.

TABLE 1. Summary of C:N and stable isotope values in Chinga crab muscle tissues and in their putative food resources.

Specimen	C:N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Chinga crab muscle	3.6 (0.9)	−23.52 (0.38)	10.03 (0.63)
Ants	4.4 (0.2)	−16.94 (0.38)	8.12 (0.40)
Detritus			
Mixed	34.7	−28.73 (0.31)	3.57 (0.67)
Cissus sp.	37.0 (1.2)	−27.79 (0.09)	2.89 (0.03)
Ficus sp. fruits	39.1	−26.77 (2.82)	2.48 (0.97)
Ficus sp. leaves	47.8 (9.5)	−28.24 (1.16)	3.37 (0.39)
Hibiscus sp.	23.2	−28.94 (0.12)	3.11 (0.45)
Pittosporum sp.	53.7 (7.4)	−29.19 (0.42)	2.73 (0.85)
Syzgium sp.	87.2 (7.9)	−29.36 (1.81)	4.14 (1.11)
Stream invertebrates			
Baetidae	5.3 (0.2)	−26.00 (0.34)	7.31 (0.28)
Caenidae	5.4 (0.5)	−25.51 (0.59)	7.39 (0.51)
Heptageniidae	6.1	−24.42	7.10
Hydropsychidae	6.5 (0.4)	−24.84 (0.09)	6.84 (0.20)
Tipulidae	5.8 (0.8)	−25.58 (0.54)	4.93 (0.48)
Chironomidae	5.7 (0.6)	−24.43 (0.47)	6.58 (0.91)
Coleoptera larva	6.8	−26.17	5.99

Notes: Values are means (with SD in parentheses) averaged over samples collected in both seasons. Crab samples were from replicate individuals; multiple individuals were pooled in samples of all other taxa. Where SD has not been reported, insufficient replicates were available for meaningful variance estimates.

were shredded by the crabs into pieces of ~2–4 mm². Occasionally, aquatic microorganisms (e.g., diatoms) occurred with the detritus, indicating that crabs obtained detritus from the stream channel. These microorganisms were sufficiently scarce, however, that accidental consumption seems likely and algivory unlikely (cf. Lancaster et al. 2005).

Diet composition varied temporally (Fig. 4), although preliminary analyses indicated no age- or sex-specific differences. All sizes of crab, from the smallest to the largest (3.0–25.0 mm carapace width), had ants in their stomachs. Detritus dominated the diet in the dry season (October–February), ants were dominant or codominant at other times, and there was no conspicuous seasonal pattern in the relative abundance of other invertebrates.

Variance in isotope values among crabs was generally low (Table 1), and preliminary analyses indicated that $\delta^{13}C$ and $\delta^{15}N$ values of crab muscle did not vary significantly with sex, maturity, or season. The absence of these factor effects was not attributable to low statistical power. The effect size detectable by statistical tests (difference between mean isotope values of any two groups of crabs) varied among comparisons, but the largest minimum effect size was 0.72‰ and 0.32‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively. Given that trophic shifts in isotopic values are commonly in the order of 2–3‰ and 1‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively (McCutchan et al. 2003), our analyses had sufficient power to detect these numerically small, but ecologically meaningful differences. Also, there was no obvious seasonal variation in the isotope values of detritus or aquatic invertebrates, so data from the two seasons were pooled to provide annual means (Table 1). The various types of detritus (leaf species) differed chemically but, compared to other

putative food resources, detritus had the highest C:N values and the lowest isotope values for both carbon and nitrogen. Crab muscle had the highest $\delta^{15}N$ and $\delta^{13}C$ values that were intermediate between those of ants and detritus. Isotope values for aquatic invertebrates were intermediate between those of detritus and of crabs. Variations in isotope values within each major food group (detritus, freshwater invertebrates, ants) were smaller than between groups, indicating isotopically distinct food sources. Therefore, mixing models used annual mean values for each of the main three food groups and crabs (the consumer).

Mixing models did not detect a significant contribution of freshwater invertebrates to crab diet. Using dual-isotope models, three food resources (ants, detritus, aquatic invertebrates) and f_C values ranging around 2.0 (as reported by Rudnick and Resh 2005), the only unique model solutions required high f_N for both food sources and implausibly high f_N for low C:N resources, i.e., $f_N > 4.0$ in contrast to the 1.0–2.9 reported for low C:N resources (Rudnick and Resh 2005). Further, these models estimated that >30% of the assimilated diet was derived from freshwater invertebrates, a value inconsistent with the volume of freshwater invertebrates in stomach contents, ~4% (Fig. 4). Although algebraically correct, we suggest that these model solutions are ecologically spurious, and aquatic invertebrates were excluded from subsequent analyses.

Dual- and single-isotope models using two food sources both indicated that ants were nutritionally important to crabs. Dual-isotope models assume that equal proportions of C and N are assimilated from each food source and, assuming that f_C does not vary with C:N of the resources (Rudnick and Resh 2005), then the
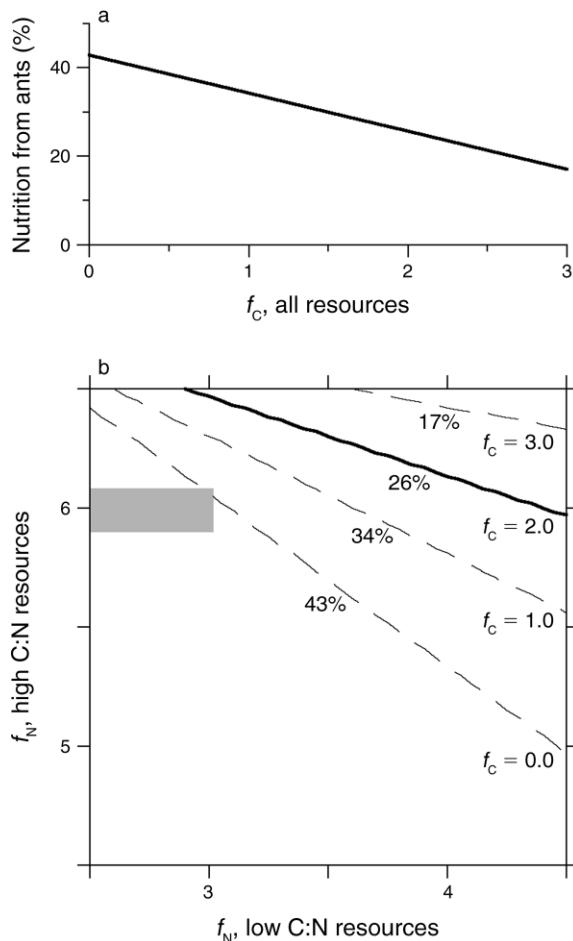
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failed to provide a model solution. The failure of dual-isotope models suggests that crabs derived C and N independently from different food sources and, thus, single-isotope models may be more suitable to assess resource assimilation. Using the fractionation values of Rudnick and Resh (2005), single-isotope models estimated ant-derived nitrogen in the range 50–90% (Fig. 6a) and ant-derived carbon of ~31% (Fig. 6b). Average fraction rates of $f_C = 1.3$ and $f_N = 2.3$ indicated even higher proportions of ant-derived nutrition.

FIG. 5. Results of dual-isotope mixing models with two food sources (ants and detritus), assuming that equal proportions of C and N were assimilated from each food source and that C fractionation, f_C, is constant across resources. (a) Percentage of Chinga crab nutrition derived from ants in relation to f_C. (b) Contour plots illustrating the percentage of ant-derived nutrition over a range of N fractionation values, f_N. The solid contour line (26% ant-derived nutrition) corresponds to $f_C = 2.0$, the fractionation value reported by Rudnick and Resh (2005) for decapod muscle. Dashed lines show other percentage estimates of ant-derived nutrition at different values of f_C, as shown in (a). The gray box indicates the previously recorded range of f_N for decapod muscle, i.e., $f_N = 1.0$–2.9 or 6.0 for crabs fed low and high C:N diets, respectively (Rudnick and Resh 2005).

dual-isotope model estimated that ant-derived nutrition was <43% (Fig. 5a). At $f_C = 2.0$, ant-derived nutrition was 26%. A range of resource-specific f_N values could estimate a total of 26% ant-derived nutrition (solid contour line in Fig. 5b), but model solutions did not encompass f_N values similar to those recorded by Rudnick and Resh (2005), even if f_C was allowed to deviate from 2.0 (dashed contour lines in Fig. 5b). Furthermore, even the average fractionation values of $f_C = 1.3$ for muscle tissue and $f_N = 2.3$ reported for consumers in aquatic systems (McCutchan et al. 2003)
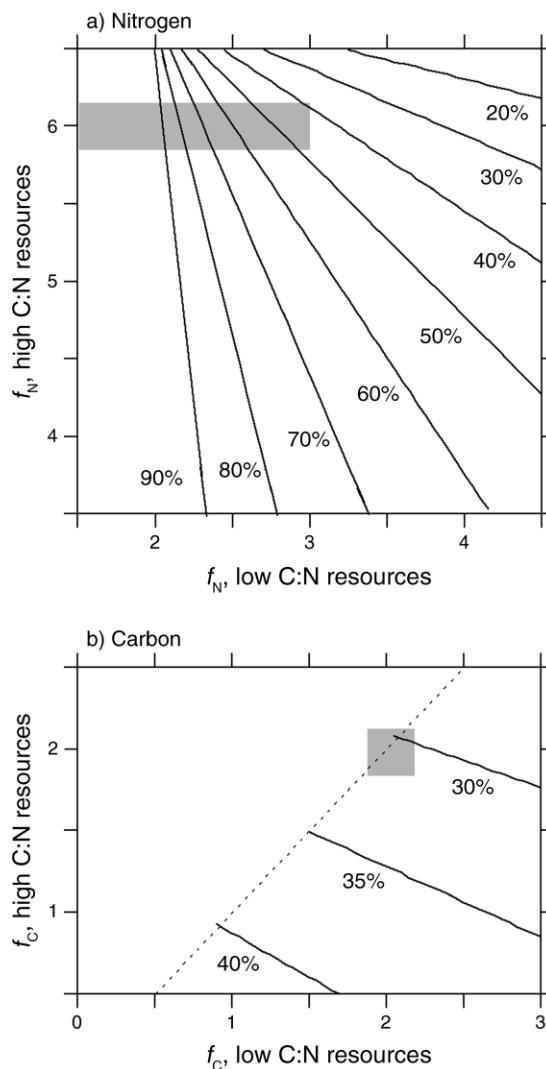

FIG. 6. Single-isotope mixing models with two food sources (ants and detritus), assuming that the proportions of C and N assimilated from each food source are independent. The contour plots illustrate the percentage of (a) ant-derived N and (b) ant-derived C over a range of fractionation values, f_N and f_C. Gray boxes indicate the previously recorded range of fractionation values for decapod muscle (Rudnick and Resh 2005): (a) $f_N = 1.0$–2.9 or 6.0 for crabs fed low and high C:N diets, respectively; (b) $f_C = 2.0$. Models assume that f_C may be lower (but not higher) for high C:N than low C:N resources. The dotted line in (b) indicates models in which fractionation values were the same for both resources.

DISCUSSION

The Chinga crab is a true omnivore and appears to be a super-dominant species in the Chinga River, where its diet consisted almost entirely of spatial subsidies: terrestrial detritus and ants. In situ prey (aquatic invertebrates) comprised a minute proportion of crab diet, perhaps reflecting their scarcity in this community. Other diet studies on lotic crabs suggest an omnivorous diet of detritus and freshwater invertebrates (Williams 1962, 1965, Hill and O'Keefe 1992), but we know of no reports of substantial prey subsidies from terrestrial invertebrates. Where terrestrial invertebrates have been recorded in crab and crayfish diets, they are typically low in abundance (Williams 1962, Parkyn et al. 2001). We found no evidence for ontogenetic variation in crab diet, unlike studies of some other freshwater decapods (crabs, Williams 1962, 1965, Hill and O'Keefe 1992; crayfish, Parkyn et al. 2001). Either the maximum size of this small-bodied crab is below the threshold at which capturing freshwater invertebrates becomes difficult, as is the case for some crabs (Williams 1965), or the manner in which crabs collect ants is size-independent.

Ants were nutritionally important to this crab population: they constituted ~35% of the annual diet (by stomach content volume) and, according to stable isotope analyses, ants were the primary source of nitrogen with detritus the primary carbon source. The implausible solutions of dual-isotope mixing models suggest that carbon and nitrogen are derived from different food sources by these omnivores (Stenroth et al. 2006), and, indeed, nitrogen assimilation by land crabs is lower on plant than animal resources (Wolcott and Wolcott 1984, 1987). Accordingly, our mixing-model estimates employed fractionation values corresponding to the C:N value of the food source (Adams and Sterner 2000, Rudnick and Resh 2005). Single-isotope models estimated that ant-derived carbon in crab muscles was ~31%, whilst ant-derived nitrogen was higher at 50–90%. In the absence of empirically derived fractionation values for the Chinga crab, our estimates of ant-derived nutrition remain approximate, but the evidence is clearly that ants are of significant nutritional value to these crabs. Other crabs (Kennish 1997, Buck et al. 2003) and stream insects (Lancaster et al. 2005) can also derive substantial nutritional benefit from both plant and animal material, so the pattern of true omnivory is not without precedent in stream invertebrates.

It is possible that Chinga crabs foraged on ants in the terrestrial environment but, more likely, they consumed ants that had fallen into the stream. Foraging movements of consumers across habitat boundaries is common and includes some freshwater invertebrates (e.g., Erman 1981). Many lotic crabs are semi-aquatic to a degree and will leave the water to feed or in response to environmental stress (for a review see Dobson 2004). The abundance of ants in the diet, however, would require frequent and/or prolonged forays on land by many individuals, and these forays would have to focus on areas of high ant activity (e.g., ant nests or trails), to the exclusion of other invertebrates. Despite searching and trapping, we observed crabs on land only rarely and during disturbances (e.g., spates). Furthermore, the diatoms associated with the detrital component of their diet suggest foraging within the stream. In contrast, ants are well-represented in the drift in some Kenyan streams (Mathooko and Mavuti 1992). Many Pheidole are seed harvester ants, but most species in moist tropical Africa are omnivorous (Taylor 2006) and could occur in any part of the riparian habitat. Ants were very abundant and active for most of the year (especially during rainy periods); trails connected nests with the nearest water body and often crossed the stream via emergent stones and woody debris. Ants could have been dislodged from these sources and, indeed, we routinely observed live ants floating on the water surface. Commonly, tens to hundreds of ants were aggregated in small eddies and dead zones along the channel, often associated with accumulations of detritus. This stream is shallow and crabs presumably scoop up these ant aggregations whilst remaining on the streambed, although we lack direct observations of crab feeding. The scarcity of other terrestrial insects in the crab diet may reflect the overwhelming abundance and activity of ants in the riparian zone.

This spatial subsidy to a dominant species is unusual and differs in several ways from more commonly described subsidies. In this discussion, we focus on the prey subsidy (ants) rather than detritus, as animal prey are likely to be key, nutritionally, to high crab density and biomass (see *Introduction*).

(1) Unlike some other terrestrial–freshwater prey subsidies, this appears to be a one-way rather than a reciprocal subsidy (Nakano and Murakami 2001, Baxter et al. 2005). Ants subsidized the diet of crabs, but a significant flux of energy from the aquatic to the terrestrial system was not apparent. Aquatic insects were so scarce that the biomass of emerging adults is likely to be low and these crabs have no obvious terrestrial predators (Dobson et al. 2007a).

(2) Crabs consumed plant and animal resources, but diet width was narrow with respect to animal prey (ants only), and we suggest that these crabs employed a rather special foraging behavior (scooping ants from the water surface). In contrast, terrestrial invertebrates can comprise large proportions of the diet and energy budget of other aquatic consumers (e.g., fishes: Nakano and Murakami 2001) but, typically, they consume a wide range of prey taxa (Nakano et al. 1999) and forage opportunistically. Reports of terrestrial invertebrates in the diet of aquatic invertebrates are scarce, but also suggest opportunistic feeding and a diverse range of prey (Townsend and Hildrew 1979, Parkyn et al. 2001; J. Lancaster, *unpublished data*).

(3) Crabs appear to have no alternative animal prey or are unable to switch prey. Ant consumption was

consistently high throughout the year, but the diet was almost exclusively detritus during the dry season when ants were inactive. There was no evidence of a change in diet or foraging behavior during this period of low ant abundance. More commonly, spatially subsidized consumers feed on in situ as well as subsidized prey, perhaps with seasonal variations in their relative abundance and consequent variations in foraging strategy (Nakano and Murakami 2001). The very existence of the Chinga crab community suggests that it is stable but, curiously, it lacks the features known to stabilize some subsidized food webs, such as a wide feeding niche (e.g., Huxel and McCann 1998), temporal variations in in situ vs. ex situ prey (Takimoto et al. 2002), or rapid behavioral responses of consumers to changing resource conditions (McCann et al. 2005).

What is the relationship between crabs and other aquatic invertebrates? Aquatic invertebrates are potential prey (they occurred in stomach contents) but they contributed little to crab diet, suggesting that Fig. 1b may best describe the flow of food resources to crabs. The paucity of aquatic invertebrates in the benthos, relative to other Kenyan streams (Dobson et al. 2002), is consistent with strong top-down predation (Fig. 2a). Despite the near-absence of aquatic invertebrates from the diet of any individual crab, the sheer number of crabs could result in diffuse but significant predation pressure at the population level. Thus, top-down control may be strong from the perspective of other aquatic invertebrates even though they were a negligible component of crab diet. Alternatively, aquatic invertebrates may be scarce for some other reason, such as predator-induced avoidance by egg-laying females (Brodin et al. 2006). Our survey results were unable to discriminate between these and other mechanistic explanations, and direct tests are now required.

The Chinga crab population appears to be donor controlled, but the processes that set the upper limit to population size are unclear. In the absence of top predators or any evidence of cannibalism or density-dependent intraspecific interactions (Dobson et al. 2007a), we speculate that population size is limited by energy constraints. Limits might be set by the crabs' ability to catch ants and consume these nitrogen-rich resources, their digestive efficiency, and their reproductive efficiency, despite year-round breeding (Dobson et al. 2007a). There appears to be no recipient control in this system (crabs do not influence ant abundance), but crabs are likely to be vulnerable to any impacts on the riparian vegetation (source of detritus) and especially to the ant population (its primary source of nitrogen). If the ant subsidy ceased, it is debatable whether this crab population would survive. In the short term, a dramatic reduction in crab population size seems inevitable, either through mortality, migration, or reduced fecundity. As a consequence, this may result in decreased detritus-processing rates and a gradual increase in aquatic invertebrate abundance. As the Chinga crab is new to

science, we cannot ethically carry out manipulative experiments on this system to test these hypotheses until the crab's distribution and conservation status has been established. However, an uncontrolled test may occur in the near future, given the current pressures on land and routine clearance of riparian vegetation in Kenya, including the Chinga River, where it flows through subsistence farms. We can but hope that a newly discovered species does not become extinct as a result.

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