COUPLING STABLE ISOTOPES WITH BIOENERGETICS TO ESTIMATE INTERSPECIFIC INTERACTIONS

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Abstract. Interspecific interactions are often difficult to elucidate, particularly with large vertebrates at large spatial scales. Here, we describe a methodology for estimating interspecific interactions by combining stable isotopes with bioenergetics. We illustrate this approach by modeling the population dynamics and species interactions of a suite of vertebrates on Santa Cruz Island, California, USA: two endemic carnivores (the island fox and island spotted skunk), an exotic herbivore (the feral pig), and their shared predator, the Golden Eagle. Sensitivity analyses suggest that our parameter estimates are robust, and natural history observations suggest that our overall approach captures the species interactions in this vertebrate community. Nonetheless, several factors provide challenges to using isotopes to infer species interactions. Knowledge regarding species-specific isotopic fractionation and diet breadth is often lacking, necessitating detailed laboratory studies and natural history information. However, when coupled with other approaches, including bioenergetics, mechanistic models, and natural history, stable isotopes can be powerful tools in illuminating interspecific interactions and community dynamics.

Key words: apparent competition; Aquila chrysaetos; *competition; predation;* Spilogale gracilis; *stable isotopes;* Urocyon littoralis.

INTRODUCTION

The role of trophic interactions in the distribution, abundance, and dynamics of organisms is a unifying theme that runs through many aspects of ecology. Direct interactions, such as competition and predation, have long been known to be important community drivers, and indirect interactions have also been shown to be important in some systems (Estes et al. 1998, Tokeshi 1999, Springer et al. 2003). Both direct and indirect interactions can be difficult to elucidate. Recently, stable isotopes have been used to offer ecologists another potential tool to help expound species interactions.

Species interactions, such as competition for food resources, can be explored using traditional approaches (e.g., diets can be reconstructed through analysis of stomach or fecal contents) or with relatively recent developments, including stable isotopes. Both traditional and contemporary methods provide a limited perspective alone, but in tandem these methods can often be complementary. Indigestible prey remains in feces or undigested remains in stomachs can be used to construct indices of how frequently foods are consumed, but it is difficult to estimate the volume consumed and impossible to estimate the amount assimilated (Kruuk and Parrish 1981, Hilderbrand et al. 1996). Moreover, these indices provide information on the taxa being consumed during the time immediately preceding capture or over seasons thus requiring repeat sampling. Stable isotope analyses provide information on assimilated foods (not just ingested foods) and represent time-integrated information regarding foods assimilated (Tieszen et al. 1983). Stable isotopes can be used to reconstruct diet, because the isotopic composition of the consumer's tissues can often be related to the isotopic composition of their diet, especially so for the ratio of stable isotopes of carbon (^{13}C:^{12}C) and nitrogen (^{15}N:^{14}N) (Hilderbrand et al. 1996, Post 2002, Kasai and Nakata 2005).

Mathematical models can then be used to quantify the fractional contribution of isotopes from a food source(s) to a consumer's diet (BenDavid et al. 1997*a*, *b*, Szepanski et al. 1999, Phillips 2001, Phillips and Koch 2002, Philips and Gregg 2003). With these models, the proportional contributions of $n + 1$ different sources can be uniquely determined by the use of n different isotope tracers (e.g., $\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$). Previous models, either based on standard linear mixing models (Phillips 2001) or on Euclidean distances (BenDavid et al. 1997*a*, *b*, Szepanski et al. 1999) did not prove satisfactory for different reasons. In particular, with more potential sources than elements analyzed, these mixing models could not provide a unique solution. To cope with this problem, Phillips and Gregg (2003) developed a source-partitioning model (Iso-Source) to calculate all feasible combinations of resources that could explain the consumer's isotopic signature in terms of its diet.

Here, we extend an approach first suggested by Nagy (1987) to couple estimates of diet with energetic expenditure to assess competitive and predatory interactions. We illustrate this approach by using a model of the population dynamics and species interactions of a well-studied suite of vertebrates on Santa Cruz Island, California, USA. Using detailed diet information, forensic investigations, and observations of prey captures, we determined the major prey items consumed by three vertebrate predators: the island fox (*Urocyon littoralis*), the island spotted skunk (*Spilogale gracilis amphiala*), and the Golden Eagle (*Aquila chrysaetos*). We then analyzed the isotopic signature of both resources and consumers using the most recent mass balance isotope model (Phillips and Gregg 2003) to determine the relative contributions of resources to the isotopic signature in the consumers' diet. Next, diet was coupled with energetic expenditure to estimate food consumption (Nagy 1987, Nagy et al. 1999). Food consumption was used to determine annual rates of the following interspecific interactions: (1) degree of resource competition between the fox and the skunk; (2) predation of foxes, skunks, feral pigs (*Sus scrofa*), and seabirds by eagles; and (3) apparent competition between pigs and native mammalian prey linked through eagle predation. Estimates of competition and predation were then used in a mechanistic model of the population trajectories of these vertebrate species (Roemer et al. 2002). Last, we used a sensitivity analysis to assess how variation in parameter estimates generated by the isotopic model influenced the result of our mechanistic model.

By combining observational, diet, isotopic, energetic, and modeling methods, we were able to elucidate complex interspecific relationships in a relatively simple trophic web that are consistent with natural history observations in the field. This approach holds potential to be widely applicable in a variety of ecological settings (Fig. 1).

MATERIALS AND METHODS

Determination of diet

Important prey consumed by the island fox and island spotted skunk were determined from the literature (Laughrin 1977, Crooks and Van Vuren 1995, Moore and Collins 1995, Roemer et al. 2001a). Whereas skunks are completely carnivorous, foxes are omnivorous. Deer mice (*Peromyscus maniculatus*) and Jerusalem crickets (*Stenopalmatus fuscus*) make up a substantial portion of the diets of both the skunk and fox, and the fox also consumes Toyon berries (*Heteromeles arbutifolia*) and other fruits.

Remains from a Golden Eagle nest discovered on Santa Cruz Island included bones of at least two island foxes, five feral piglets, and three bird species (Common Raven [*Corvus corax*], Brandt's Cormorant [*Phalocrocorax penicillatus*], and Western Gull [*Larus occidentalis*]; Roemer et al. 2001a). Eagles that had been live captured for relocation smelled of skunk, suggesting skunks as prey items as well. Although we knew that eagles fed upon at least six different prey items, we were most interested in their consumption of mammalian vs. avian prey. Indeed, eagles are having a deleterious impact on the fox, having driven three of six populations toward extinction (Roemer et al. 2001a, Courchamp et al. 2003, Roemer and Donlan 2004, Roemer et al. 2004, U.S. Fish and Wildlife Service 2004).

Stable isotope analyses

Isotope values (δ^{13}C and δ^{15}N) for Golden Eagle breast feathers, plasma blood samples (for foxes, skunks, and pigs), rodent muscle, whole Jerusalem crickets, and Toyon fruits collected from Santa Cruz Island (Appendix: Table A1) were determined using a Carlo Erba Model NA 2500 elemental analyzer coupled to a Finnigan Delta Plus isotopic ratio mass spectrometer (both from Thermo Electron Corporation, Waltham, Massachusetts, USA) at the Colorado Plateau Stable Isotope Laboratory, Northern Arizona University (Flagstaff, Arizona, USA). Seabird isotope signatures were from egg albumen collected from the Farallon Islands located 500 km north of the Channel Islands (Sydeman et al. 1997). While the tissue and location of the seabird values are not ideal, they serve as valid proxies to assess the relative contribution of marine and terrestrial components to the eagle diet. Similar values were reported for gulls and cormorants from different tissues (bone and muscle) that would presumably be consumed by eagles during feeding (Kelly 2000).

We estimated prey source contributions using a mass balance mixing model that determines the distribution of all possible source contributions in systems where the number of sources is greater than $n + 1$, n being the number of isotopes used (Phillips and Gregg 2003). The mass balance approach produces a range of values rather than focusing on a single value such as the mean (Phillips and Gregg 2003); these ranges of values were then used as boundaries for the mathematical model. We adopted isotope fractionation values from the literature: 3‰ for nitrogen and 2‰ for carbon when vertebrate prey and berries were consumed, and 1‰ when invertebrates were consumed (Deniro and Epstein 1981, Schoeninger and Deniro 1984, BenDavid et al. 1997a, b, Drever et al. 2000).

Estimates of daily food consumption: competition and predation

Competition coefficients, β_{sf} and β_{fs}, where the subscript sf denotes the impact of a fox on a skunk and the subscript fs denotes the reciprocal impact, were estimated by determining field metabolic rates (FMR) based on an allometric equation for carnivores (Nagy et al. 1999):

$$FMR = 2.23M^{0.85}$$

where M is the average body mass of the carnivore. The average mass of Santa Cruz Island foxes and skunks are: male fox, 2.00 ± 0.23 kg ($n = 77$); female fox, 1.81 ± 0.22 kg ($n = 77$); male skunk, 620 ± 40 g ($n = 5$); and
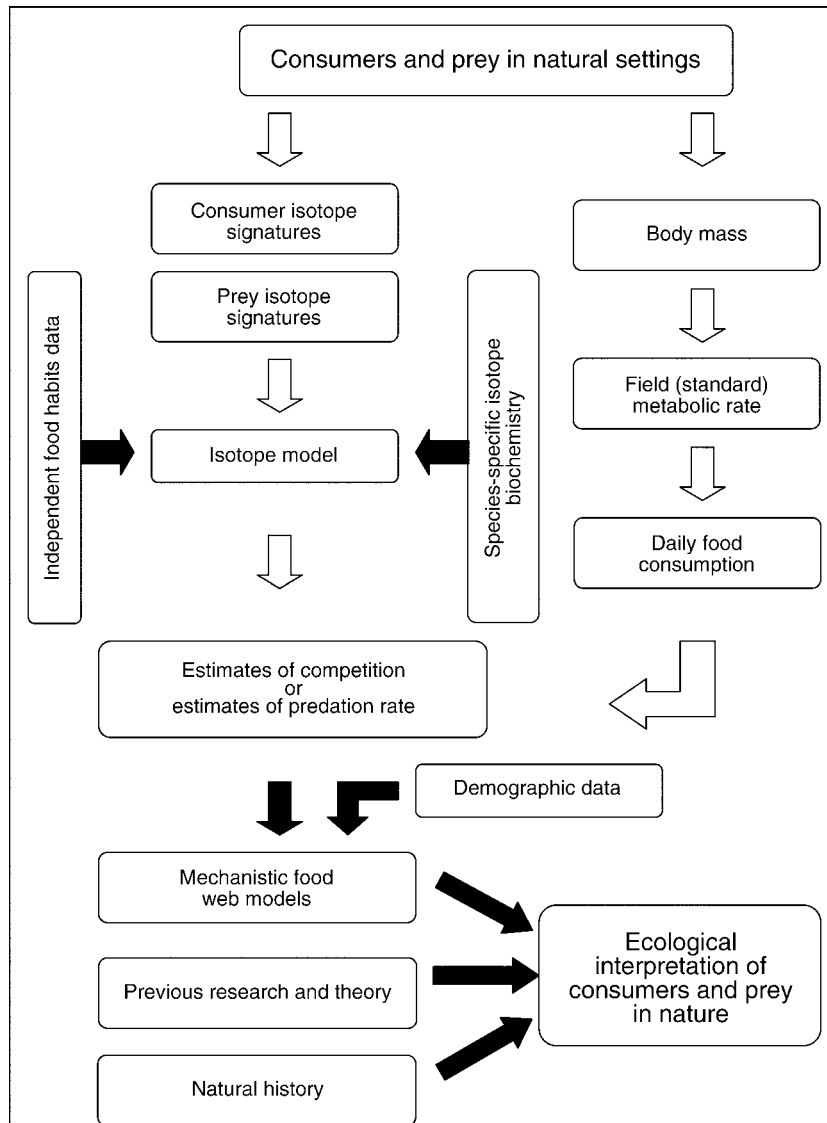
FIG. 1. Flow diagram to estimate interspecific interactions using stable isotopes and bioenergetics. We begin with a suite of focal consumers and their prey (resources); open arrows indicate a loss of information to the next step, whereas solid arrows indicate a gain of information to the next step. The desired endpoint is a correct interpretation of species interactions. Examples of loss of information include tissue routing and unknown fractionation values (isotope signatures), inability to include all potential prey (isotope model), limited estimates in time and space (body mass), summation of energetic expenditure over large time frame, costs of individual behaviors unknown (field metabolic rates), unknown prey item proportion actually consumed, digested, and assimilated (daily food consumption), and lack of species interaction understanding if prey are limiting (competition/predation).

female skunk, 500 ± 40 g ($n = 4$) (mean ± SD; Crooks 1994, Roemer 1999).

Estimates of FMR (kJ/d) were converted to daily food consumption (DFC, g DM/d, where DM is dry mass) using estimates of metabolizable energy for omnivores (14.0 kJ/g DM) and carnivores (16.8 kJ/g DM), respectively (Nagy et al. 1999). We assumed that skunks were completely carnivorous, and we determined the amount of animal food in the diet of the fox using the isotope model. Estimates of fresh animal matter consumed (3.33 g FM/1 g DM) were calculated from dry animal matter consumed. Competition coefficients

were determined by taking the ratio of the amount of fresh animal matter consumed by the pair of competitors (i.e., β_{sf} is fresh animal matter consumed by a pair of foxes divided by fresh animal matter consumed by a pair of skunks, whereas β_{fs} is the reciprocal of this value). Although this measure of bioenergetic dietary overlap clearly represents only one dimension of a competition coefficient, we were unable to evaluate other potential components of the dynamic that may exist between these two species (Crooks and Van Vuren 1995).

Predation rates by eagles on their main prey were determined in a similar fashion. We first estimated the

standard metabolic rate, SMR (W/kg), of a Golden Eagle from environmental data measured on Santa Cruz Island from June 1995 through July 1998 (Hayes and Gessaman 1980):

$$SMR = 1.163(6.1168 - 0.06W - 0.0793T_a \\ - 0.955 \times 10^{-3}IR + 0.1284U)$$

where W is body mass (kg), T_a is ambient temperature (°C), IR is incident radiation (W/m^2), and U is wind speed (m/s). SMR was converted from W/kg to kJ·bird^{-1}·d^{-1} adopting a Golden Eagle weight of 4.0 kg. SMR is an average daily estimate of the amount of energy expended by an eagle as a consequence of thermoregulation in the face of variable climatic conditions.

Estimates of SMR were incorporated into a time–energy budget to estimate daily energy expenditure (DEE) and ultimately DFC of an eagle (g·bird^{-1}·d^{-1}; Stalmaster and Gessaman 1984, Collopy and Edwards 1989). Eagles were assumed to spend a 24-h period in various activities including feeding and other maintenance behaviors, perching, active flight, soaring or in passive flight and roosting. We assumed that eagles roosted for 12 h and for the remaining 12 h we adopted an activity budget for nesting Golden Eagles (Collopy and Edwards 1989). This activity budget was then incorporated into a time–energy budget originally designed for Bald Eagles (*Haliaeetus leucocephalus*; Stalmaster and Gessaman 1984). Estimates of SMR were used when an eagle was inactive; when eagles were active, we negated the effects of climate and assumed that the cost of active flight was 12.5 times that of basal metabolic rate (BMR) and that the cost of passive flight was 3.5 times that of BMR (Gessaman 1987). Wet-matter energy of a mammal was 6.03 kJ/g (Collopy 1986). After determining DFC for an actively foraging, adult Golden Eagle on Santa Cruz Island, we used the diet composition estimated from the isotope model to estimate how many prey items an eagle was consuming to meet its energetic requirements.

A measure of the strength of apparent competition was obtained through the use of preference coefficients (Φ and σ), where Φ is a measure of an eagle's preference for native foxes relative to piglets and σ is a measure of an eagle's preference for native skunks relative to piglets (Roemer et al. 2002). Preference coefficients were calculated by first determining the proportion of prey in the diet of the eagles with the mixing model, then dividing the ratio of prey i in the eagle diet by the carrying capacity K_i to account for prey abundance, and finally, dividing the values obtained for foxes and skunks by that obtained for piglets to estimate Φ and σ, respectively (see Roemer et al. 2002 for parameter estimates).

Mechanistic model and sensitivity analysis

Estimates of competition and predation were used to parameterize a Lotka-Volterra population model to explore the dynamics between the Golden Eagle and its three mammalian prey (foxes, skunks, and pigs [Roemer et al. 2002]). Equations of the model are as follows:

$$\begin{cases} \dfrac{dF}{dt} = r_f F\left(1 - \dfrac{F + \beta_{fs}S}{K_f}\right) - \mu_f \dfrac{\phi F}{\phi F + \sigma S + P}EF \\[2ex] \dfrac{dS}{dt} = r_s S\left(1 - \dfrac{S + \beta_{sf}F}{K_s}\right) - \mu_s \dfrac{\sigma S}{\phi F + \sigma S + P}ES \\[2ex] \dfrac{dP}{dt} = r_p P\left(1 - \dfrac{P}{K_p}\right) - \mu_p \dfrac{P}{\phi F + \sigma S + P}EP \\[2ex] \dfrac{dE}{dt} = \dfrac{(\lambda_f \mu_f \phi F^2 + \lambda_s \mu_s \sigma S^2 + \lambda_p \mu_p P^2)E}{\phi F + \sigma S + P} - \nu E. \end{cases} \quad (1)$$

In brief, each prey population i is characterized by its intrinsic growth rate (r_i), its carrying capacity (K_i), an energetic measure of resource competition (β_{ij}, for foxes and skunks only), a predation rate by eagles (μ_i), and a term of eagle preference for foxes (ϕ) and skunks (σ) relative to piglets. If ϕ or σ are greater than 1, eagles prey more often on foxes or skunks than on piglets, respectively. Eagle mortality rate is ν and the rate at which prey i are turned into new predators is given by λ. Previously, we reported a sensitivity analysis of the competition coefficients (β_{sf} and β_{fs}), and the preference coefficients (ϕ and σ) that were estimated from an Euclidean isotope, mixing model (Roemer et al. 2002). The mechanistic model appeared robust when these focal parameters were altered ±10%. Here, we extend the sensitivity analysis by including all four parameters (β_{sf}, β_{fs}, ϕ, and σ) from the range of all values obtained from a mass-balance isotope, mixing model. Because some parameters (e.g., Φ and σ) vary by much more than 10% (see *Results*), a lack of a drastic change in the output parameters would reflect the robustness of the mechanistic model and our overall approach.

RESULTS

Trophic relations and diet composition

The distribution of feasible diet proportions was well constrained and informative for both the island fox and the Golden Eagle. Stable isotope results depicted proportions of animal food in the fox diet that were concordant with food habits information derived from fecal analysis in the broad sense: 65–72% of the fox diet was animal and 28–35% of the diet was plant food. This is concordant with previous results found using a Euclidean isotope model (77% animal and 23% plant; Roemer et al. 2002).

For the eagle's diet, all four resources formed a polygon in the center of which laid the consumer. Seabirds showed a distinct marine signature with elevated $\delta^{13}C$ and $\delta^{15}N$, and appeared to form a low percentage of the eagle's diet (1–99th percentile: 0–9%). Pig, fox, and skunk all formed a larger part of the eagle's diet (1–99th percentile: 28–90%, 0–51%, and 0–23%, respectively). Combined with the lack of marine
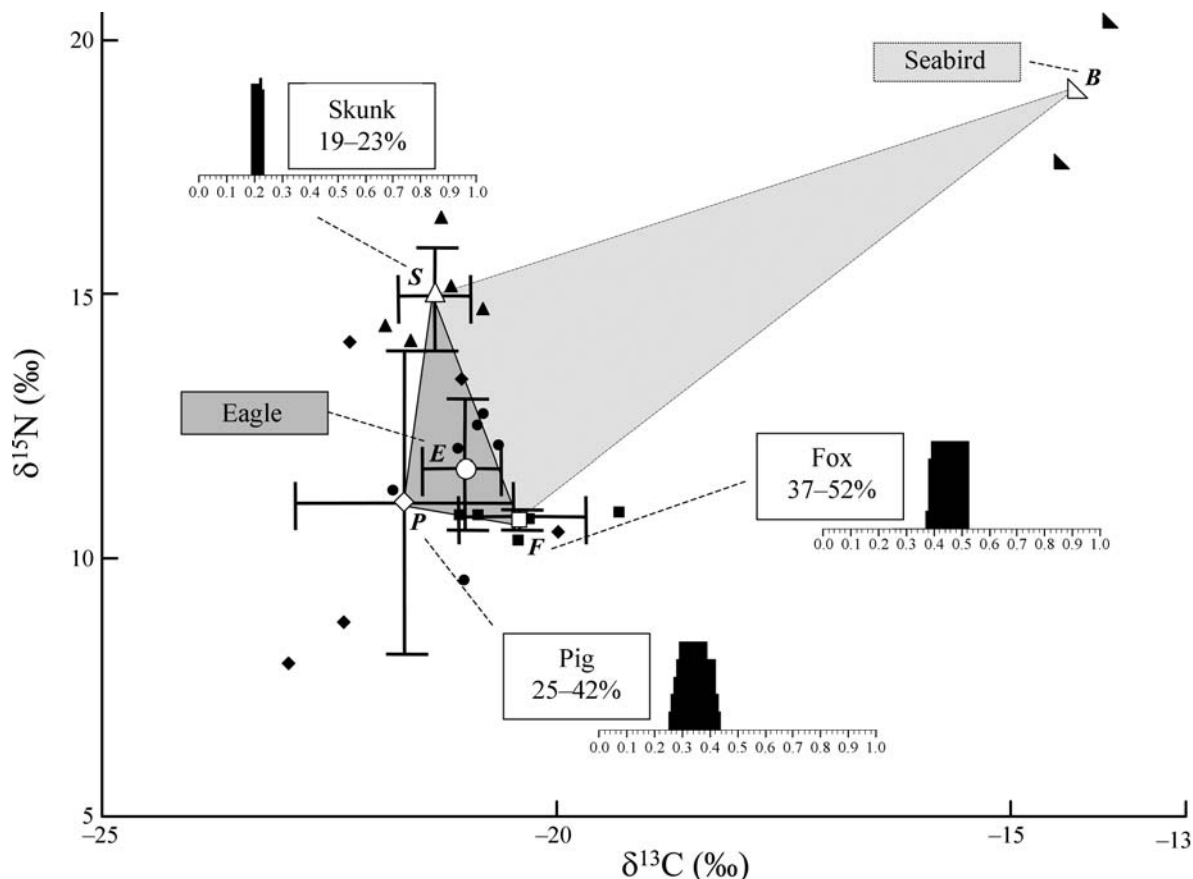
FIG. 2. Signatures for $\delta^{15}N$ and $\delta^{13}C$ of four prey for Golden Eagle (from Santa Cruz Island, California, USA) and mixing polygon (light gray) circumscribed by the isotopic signatures of the prey with respect to the individual signatures of the Golden Eagle (after correcting for trophic fractionation). Skunks are shown by triangles, foxes by squares, pigs by diamonds, and eagles by circles. Solid symbols are measured values, open symbols are means, and error bars show SE. Histograms show the distribution of feasible contributions from each source to the eagle diet. Values shown in the boxes are 1–99th percentile ranges for these distributions. Seabirds are a minor prey item of Golden Eagles and are thus neglected in further analysis: only the three species forming the darker triangle are considered.

signature in the Golden Eagle feathers (i.e., the distance between eagle and seabird isotope signatures), the isotope models suggest that seabirds contributed little to the diet of Golden Eagles (Fig. 2). This result is consistent with field observations in other locales (Hunt et al. 1980), but is discordant with respect to prey remains discovered in eagle nests on Santa Cruz Island (Roemer et al. 2001a). When avian prey is removed from the model, fox constitute the majority of the eagle's prey (37–52%), pigs remain an important secondary food source (25–42%), whereas skunks remain the least important mammalian prey (19–23%). All of these findings are consistent with previous results where the Euclidean model predicted 51% fox, 34% piglet, and 15% skunk (Roemer et al. 2002).

With the range of possible contributions estimated for each prey species, the range of the preference coefficients of an eagle for either a fox or a skunk relative to a piglet was from 4.52 to 11.18 (ϕ) and from 2.32 to 4.94 (σ), respectively. Despite the relatively large range possible for

these two parameters, which represent a measure of the strength of apparent competition, the qualitative results of the mechanistic model did not change (the relative proportions of individuals remained the same), and the quantitative outcome (the number of individuals) changed only moderately (Appendix: Fig. A1). In all cases of ϕ and σ, the fox numbers decline dramatically, and skunk numbers increase (compared to when there are no pigs), so that both carnivore populations are similar in size.

Estimates of daily food consumption and competition in foxes and skunks

The mean predicted field metabolic rate (FMR) for a male fox was 1426 kJ/d (95% CI = 601–3381) and for a female fox was 1310 kJ/d (95% CI = 618–2773). Predicted FMR for a male skunk was 527 kJ/d (95% CI = 139–1977) and for a female skunk was 439 kJ/d (95% CI = 113–1683). Thus, the mean predicted FMRs for a pair of foxes (2736 kJ/d) was nearly three times greater than that predicted for a pair of skunks (966 kJ/d).

Daily food consumption was estimated at 101.9 g DM/d and 93.6 g DM/d for a male and female fox, respectively, and 31.4 g DM/d and 26.1 g DM/d for a male and female skunk, respectively. Given that skunks are completely carnivorous, we multiplied the percentage of animal matter in the foxes diet times the estimate of DFC to determine diet overlap. We then converted the amount of dry animal matter consumed to the amount of fresh animal matter consumed (3.33 g FM/1 g DM) by both a pair of foxes and skunks. With the isotope model used, a pair of foxes consumes 429.67–468.73 g of fresh animal matter per day (percentage of animal food in the fox diet varied from 65% to 72%), while a pair of skunks consumed 191.5 g. Thus, a pair of foxes consumes more than two times the amount of fresh animal matter per day as a pair of skunks. Competition coefficients were the ratio of these values. $\beta_{sf} = 2.24$–2.45 and $\beta_{fs} = 0.41$–0.45. Here again, we used different possible values of the competition coefficients to check whether the output of the mechanistic model changed either qualitatively or quantitatively. The model predictions remain qualitatively and quantitatively similar (Appendix: Fig. A2), with the fox and skunk numbers ending up at very similar sizes.

Estimates of daily food consumption and predation by Golden Eagles

The average DFC was 461 ± 15 g·bird^{-1}·d^{-1} (mean $\pm$ SD) for an actively foraging 4.0 kg Golden Eagle resident on Santa Cruz Island. A single breeding Golden Eagle would require an additional 10.3 kg/yr based on adding the average energetic requirements of a single nestling eagle (Collopy 1986). Thus, a pair of breeding eagles that successfully fledge a single chick would consume 357.1 kg of prey tissue per year. Island foxes on Santa Cruz Island weigh 1.93 ± 0.25 kg ($n = 279$; Roemer et al. 2001b), skunks average 560 g (Crooks 1994), and piglets were assumed to weigh as much as a fox. Assuming 30% wastage of an animal weighing 1–4 kg or 20% wastage of an animal weighing <1 kg (Brown and Watson 1964), one can thus calculate a predation coefficient for each of the three mammalian prey. For example, the above data imply that eagles preying only on foxes or fox-size animals must kill 124.6 prey per year, to which we add a further requirement of 10.3 kg (=7.6 foxes) for the breeding period. This yields 132.1 foxes a year, which sets the predation coefficient on foxes, μ_f, at 0.086 (we divide the predation rate by the prey carrying capacity, $K_f = 1544$, to correct for relative abundance (Roemer et al. 2002). Similarly, we find $\mu_p = 0.019$ and $\mu_s = 0.159$ (Roemer et al. 2002). As these coefficients are species specific and not dependent on isotopic estimates, a sensitivity analysis with respect to different isotope values is not appropriate here.

With the mass-balance mixing model of Phillips and Gregg (2003), each of the potential source combinations is constrained to sum to 100%, yielding trade-offs among the sources within their feasible ranges. Using a scatter plot matrix, we can estimate the joint distribution of food sources for all feasible dietary compositions, which elucidates these trade-offs (Appendix: Fig. A4). This approach allows an estimate of the number of each prey killed by a pair of Golden Eagles (which is different from the species specific predation coefficients above). Basing the percentages of prey consumed on the mixing model, a pair of Golden Eagles would kill 114–163 foxes, 57–72 skunks, and 78–127 piglets per year, for an average of 309 ± 4.5 prey items killed annually. This equates to a single eagle making a kill approximately every 2.36 days.

DISCUSSION

In this paper, we combined isotopic and energetic analyses to obtain coefficients that estimate interspecific relationships, particularly classical and apparent competition. We then used a mechanistic model to describe the dynamics of four vertebrate species in a simple trophic web in the California Channel Islands, USA (Roemer et al. 2002) and used a sensitivity analysis to assess how robust the model was to the range of values obtained for the interspecific coefficients.

The range of possible proportions of prey in the eagle diet did have an influence on our estimates of eagle preference for different prey, measures that reflect the strength of apparent competition. Nevertheless, when we used these estimates and then simulated the changes in the vertebrate populations, we found little quantitative change in model outcome (Appendix: Fig. A3A). The same conclusion is reached for the two competition coefficients; the range of values obtained from the mixing model did not affect the model outcome (Appendix: Fig. A3B), and neither did modest changes ($\pm 10\%$) in the predation coefficients (Roemer et al. 2002). In all cases, the model still suggested that in the presence of pigs, the eagle population would increase and the pig population would be relatively unaffected. As a consequence, the fox population would decline and, once released from fox competition, the skunk population would increase; this is precisely what was observed in the field (Roemer et al. 2002). So despite relatively large changes in the estimates of the apparent and classical competition coefficients, the mechanistic model still captured the interspecific interactions and accurately depicted the dynamics of the insular vertebrate community on the Channel Islands. This suggests that using a source partitioning isotopic model such as the one proposed by Phillips and Gregg (2003) is a reliable approach for estimating parameters for the type of dynamical model we used.

As with any approach, however, there are potential sources of error and certainly room for improvement. For example, a potential problem with the application of our approach is the width of the parameter range that is provided by the source partitioning isotopic model. Although it was not the case here, this might sometimes prove problematic. In addition, our estimates of

competition were based on allometric estimates of field metabolic rate (FMR) that have large standard errors owing to the large variance in FMR across species that is unexplained by the regression approach (Nagy et al. 1999). It is possible that our estimates of FMR in the island fox and in the spotted skunk could be biased because we did not directly measure FMR in either species. A comparison of FMRs directly measured in other foxes (Geffen et al. 1992, Covell et al. 1996, Girard 2001) suggests that our estimates are reasonable and may even be conservative. Nonetheless, direct measurement of FMR of both foxes and skunks would improve upon these estimates and our approach.

Our estimates of indirect competition also assume that resources are limited and this assumption may not be valid (Paine 1966, Paine and Schindler 2002). Just because foxes and skunks use the same resources does not mean they are competing for them: resources may be hyperabundant and therefore not limiting. The premise that foxes and skunks are in competition was, however, supported by previous work (Roemer et al. 2002).

Finally, our estimates of daily food consumption and predation rate by Golden Eagles were also not measured directly. Yet, they appear realistic and are concordant with other studies that directly measured these parameters in eagles (Fevold and Craighead 1958, Love 1979, Stalmaster and Gessaman 1984).

The methodology presented here is based on a case where the trophic relationships are rather complex (e.g., apparent competition). Investigations of other trophic webs in simple ecosystems where predation is important (e.g., small invaded islands) could greatly benefit from this approach, as predation is a more readily quantified parameter.

Estimation of competition and predation can require tedious analyses of feces or stomach contents, forensic investigation, longitudinal studies of predator–prey interactions, and experimental manipulations (Paine 1966, Connell 1983, Estes et al. 1998, Fedriani et al. 2000, Terborgh et al. 2001). Such approaches require extensive investment of time and money and may not be possible, particularly at large scales or with large vertebrates. This is especially true for indirect relationships such as apparent competition for which qualitative as well as quantitative characterization is problematic. We have presented an indirect approach for estimating direct and indirect interspecific interactions and for evaluating community dynamics. Our approach corroborated past and present species dynamics elucidated by our own empirical work (Roemer et al. 2001b, Roemer et al. 2002) and the work of others (Crooks and Van Vuren 1995, Coonan et al. 2000). Even relatively large changes in some of the input parameters did not have a profound influence on the qualitative outcome of our mechanistic model.

Our results suggest that, at least for some systems, stable isotopes can be used as a heuristic tool, and incorporating this tool with estimates of energetic expenditure and life history information within a functional framework can achieve a correct interpretation of species interactions. Beyond the qualitative assessment of predation that is becoming frequent in ecological studies, this also allows the characterization of direct and apparent competition rates, and could therefore form the basis of a methodology with a great potential for conceptual and functional ecology.

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APPENDIX

A figure showing response of the dynamical model to the changes in the competition coefficients or the apparent competition coefficients for the fox and skunk as conferred by the isotopic analysis, a scatterplot matrix of distribution histograms, and a table showing stable carbon and nitrogen isotope abundance of various species on Santa Cruz Island, California, USA (*Ecological Archives* A016-064-A1).