Invasions and stable isotope analysis – informing ecology and management

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Abstract Stable isotope analysis has increasingly been used to answer ecological questions. However, despite their potential, stable isotopes have rarely been used to assist with managing invasions. Here we discuss some of the principles behind the use of stable isotope analyses. We also review how stable isotopes can aid our understanding of the threats posed by invasive species, and the mechanisms by which some species successfully invade new environments. We then show how information from stable isotopes can be used to evaluate and refine ongoing management actions from an early stage in eradication attempts. We highlight the potential for such approaches to rapidly and simply provide detailed ecological information. We conclude that this technique can be used not only to inform our understanding of the problems caused by invasive species, but also to facilitate conservation and resource management objectives for wildlife populations.

Keywords: adaptive management, invasive species, island, spatial marker, trophic web

INTRODUCTION

Stable isotope analysis (SIA) has increasingly been used to answer ecological questions about organisms, including those relating to diet and migration patterns (Dalerum and Angerbjorn 2005; West et al. 2006; Crawford et al. 2008; Inger and Bearhop 2008). This focus has in turn led to an increase in the number of chemical elements used and the variety of ecological questions addressed (Fry 2006). Finer resolution to SIA has been aided by recent advances in statistical modelling (Phillips and Eldridge 2006; Parnell et al. 2010; Jackson et al. 2011). Stable isotope analyses have only recently been applied to invasion biology. This short review examines how SIA can be an additional tool to assist with the management of invasive species. We first discuss the ways SIA can be applied, then show how it can assist with studies of invasion biology as well as refining approaches to eradication campaigns.

BASICS OF STABLE ISOTOPE ANALYSIS

Many chemical elements can have more than one isotopic form of differing molecular mass. Examination of the stable isotopic ratios of the various forms of oxygen, hydrogen, sulphur and strontium have all helped to provide unique insights into the ecology and biology of plants and animals (e.g., Crawford et al. 2008), but the two most commonly used are stable isotopes of carbon (C) and nitrogen (N). The former (the ratio of 13C to 12C, expressed as δ13C) can be used to discriminate among different sources of primary production. The derivation of such ratios can potentially identify an animal’s foraging location. For example, there is a difference between marine and terrestrial sources, where marine signatures are enriched with 13C compared to terrestrial ones (Fry 2006). Stable nitrogen isotope ratios, (15N to 14N, expressed as δ15N) can also vary spatially, but are much more useful as a means for determining the trophic level at which an animal is feeding. Organisms become progressively enriched in 15N at higher trophic levels due to preferential retention of the heavier isotope during tissue synthesis (Fry 2006). As a result there is a stepwise style enrichment between consumer and prey, meaning that animals feeding at higher trophic levels within a food web have higher δ15N in their tissues than those feeding at lower trophic levels.

With the increasing use of SIA, methods have been developed to quantify the importance of multiple food sources or determine the probability of animals moving across different localities. Such methods require stable isotopic ratios from the consumer’s tissue (hair, feathers, whiskers, claw, blood, liver, bone etc), and also the stable isotope ratios of potential prey, local geology or rainfall patterns (e.g., West et al. 2006). Mixing models (Phillips and Gregg 2003) are often applied to interpret these results and, more recently, Bayesian solutions to these analyses have been developed (Parnell et al. 2010).

ADVANTAGES OF USING SIA

Many species are difficult or expensive to study in the field because of their behaviour or location. For example, the nocturnal and neophobic behaviour of rats (Rattus spp.), coupled with difficulties with accessing invaded islands can prevent detailed year-round study. Furthermore, the use of conventional techniques such as radio telemetry or scat analysis are a time consuming, labour intensive and costly method of measuring the ecological impacts of invasive species. By comparison, SIA is relatively cheap because time and effort required in the field can be reduced. This is because behavioural information can be gathered over multiple time scales through the analysis of multiple tissue types from an individual after a single capture event. Since different tissue types are replaced at different rates, the proteins within them will be synthesised at different times. The proteins then reflect aspects of the animal’s ecology at these different points. For example, stable isotope signatures from liver cells reflect the animal’s diet over previous days, those of muscle reflect the diet over preceding weeks to months, and those of hair for longer still (Kürle 2009). The length of time represented by isotopes in tissues also varies with the metabolic activity of the animal concerned. Replacement processes are more rapid in species with higher metabolic rates, so that, for example, mice have faster replacement rates than rats (MacAvoy et al. 2006).

Single tissues such as claws, whiskers and hair can also be used to derive a time series of past behaviour. The protein in these tissues is metabolically inert after it has been synthesised, so provides a continual record which can be ‘read’ along its length, going back in time the nearer a sample is to the distal end of the tissue (Bearhop et al. 2003; Cherel et al. 2009). In sum, SIA of multiple tissues of an individual animal can rapidly provide a detailed record of diet and potential foraging locations over different time scales.
DEMONSTRATING THE IMPACTS OF INVASIVE SPECIES

The accumulated knowledge of a species’ impacts elsewhere remains the best predictor of their likely effects at new locations (Simberloff 2003). However, a business case for the eradication or control of invasive species will often still require site-specific information.

Direct predatory impacts

Stable isotope analyses can be used to examine the diet of invasive predators. While this provides an integrated picture of an animal’s diet, SIA cannot be used to differentiate between predation and scavenged food items. For example, Stapp (2002) demonstrated that ship rats (Rattus rattus) in the Shiant Islands, UK consumed seabird flesh, but could not demonstrate predatory behaviour from this result. Although proof of predatory behaviour may not necessarily be derived from SIA, it has advantages over conventional methods such as stomach content or scat analyses, which may over-represent indigestible material or under-represent items that leave little visual trace. The most informative approach can be to combine SIA with other methods to strengthen the conclusions that can be drawn (Hobson et al. 1999). For example, Harper (2007) used experimental removal of ship rats and a predatory bird, weka (Gallirallus australis), alongside isotopic and conventional diet analysis to examine the importance of sooty shearwater (Puffinus griseus) in each species’ diet. Caut et al. (2008) used a combination of SIA, stomach contents and direct observations to reveal the impact of ship rats on breeding seabirds on Surprise Island, New Caledonia. They also showed how, in the absence of seabirds, rats switched prey to green turtle (Chelonia mydas) hatchlings. Hobson et al. (1999) were similarly able to demonstrate the seasonal importance of breeding seabirds in the diet of brown rats R. norvegicus on Langara Island, British Columbia, and also the extent to which different individuals relied on this resource. Such plasticity in the consumption of seabirds by individual brown rats was also found when they fed on least auklets (Aethia pusilla) at Kiska Island, Alaska (Major et al. 2007).

Impacts on trophic structure

The way that invasive species disrupt food webs and transform community structure has also been revealed through the use of SIA (e.g., Vander Zanden et al. 1999; Croll et al. 2005). Changes in trophic level can be seen through examination of changes in δ15N within a species over time, as was demonstrated for the invasive carnivorous Argentine ant (Linepithema humile) in California. Initially, invading ants occupied a similar trophic level to those in their native habitats, where they fed on other ants. However, once established, the ants shifted to a lower trophic position as they consumed more plant material following severe reductions in native ant prey populations (Tillberg et al. 2007). At a whole-island scale, Croll et al. (2005) used SIA to measure the importance of marine nitrogen input from seabirds to Aleutian Island plant communities. They found that on islands where invasive arctic foxes (Alopex lagopus) had destroyed the seabird populations, plant communities were transformed from grasslands to shrub/fork communities because of reduced soil fertility.

Invasive plants can also modify food webs. Stable isotopes (δ15N) demonstrated that invertebrates that persisted within areas invaded by the Spartina alterniflora x foliosa hybrid in San Francisco Bay, USA were consuming this invader (Levin et al. 2006). However, other invertebrates such as amphipods, which are an important prey item for many predators, were less tolerant to habitat invasion as they did not consume the hybrid plant. Thus while the invasive plant structurally altered the ecosystem, its resources were not efficiently broken down, resulting in bottom up alteration of the food web (Brusati and Grosholz 2009). Energetics modelling combined with SIA was used to demonstrate dramatic changes in a food web on the Channel Islands, California following the introduction of feral pigs (Sus scrofa) (Roemer et al. 2002). The pigs provided an abundant food resource for golden eagles (Aquila chrysaetos), which increased in number. Increased predation by eagles reduced the population of island fox (Urocyon littoralis). This in turn allowed island skunk (Spilogale gracilis amphila) populations to increase following reduced competition from foxes. The SIA also demonstrated the low level of marine input from seabirds to the eagles’ diets and their concentration, in particular, on introduced terrestrial prey.

Isotope studies are particularly useful for determining the effects of introduced fish, possibly because other techniques used for terrestrial vertebrates are often not applicable to aquatic species. SIA studies revealed how introduced salmonid species such as Oncorhynchus spp., Salmo spp., and Salvelinus spp. altered food webs by reducing prey fish abundance. This led to increased consumption of zooplankton by the invasive fish, and so to a reduction in their own trophic level (e.g., Vander Zanden et al. 1999). Introduced trout can also affect terrestrial food webs by consuming insects that would otherwise constitute important prey resources for terrestrial species. For example, trout introduced into previously fish-free lakes competed with the critically endangered mountain yellow-legged frog (Rana muscosa) for emergent insect prey (Finlay and Vredenburg 2007). Adult frogs feed on lake shores, and their consumption of emergent insects plays a key role in transferring energy between aquatic and terrestrial environments. Differences in isotopic values between benthic and pelagic prey revealed how fish altered aquatic food webs by consuming large numbers of benthic insects, largely restricting the supply of these to terrestrial environments. The importance and frequency of energy transfer between aquatic and terrestrial systems is increasingly recognised (e.g., Knight et al. 2005), and SIA is an ideal tool for examining such linkages.

Differences in niche width

Comparisons of niche width at individual and population levels can be explored with stable isotopes (e.g., Bearhop et al. 2006) and then used to predict the potential spread and range of an invader. Invasive species often show high plasticity of niche width in terms of habitat use, feeding ecology or behaviour (Hayes and Barry 2007). For example, a recent study in southern Sweden demonstrated that invasive signal crayfish (Pacifastacus leniusculus) have a potential niche width almost twice the size of the native European crayfish (Astacus astacus). However, signal crayfish often used a similarly sized niche to European crayfish within a given habitat (Olsson et al. 2009). Isotopic analyses also revealed greater plasticity in invasive plants. The invasive tree Schinus terebinthifolius in Hawaii had δ13C values indicating a much greater capacity to adjust its physiology to variation in soil water availability, and more efficient water conservation, than the native trees to which it was compared (Stratton and Goldstein 2001).

Differences between multiple invasive species have also been examined with SIA, revealing how distinctions in habitat and diet utilisation allow multiple invasions of an ecosystem. Rudnick and Resh (2005) demonstrated that while Chinese mitten crabs (Eriocheir sinensis) and
red swamp crayfish (*Procambarus clarkii*) primarily consumed plant material, crabs principally fed on aquatic algae, whereas crayfish consumed terrestrial-derived material. Likewise, Harper (2006) demonstrated how three invasive species of rats (ship rat, Pacific rats (*R. exulans*) and brown rat) on Pearl Island, New Zealand varied in their food resources and in their competitive ability to use them, allowing all three species to coexist on this small island.

**Assessing priorities**

Lastly, SIA of diets can aid the prioritisation of eradications. Once Roeper et al. (2002) demonstrated the threat that golden eagles posed to Channel Island foxes, eagles were translocated elsewhere and the best method for pig removal was implemented to avoid endangering the remaining foxes (Caut et al. 2006). In contrast, a combination of SIA, gut analyses and trapping led Quillfeldt et al. (2008) to conclude that a large breeding population of thin-billed prions (*Pachyptila belcheri*) on New Island, Falkland Islands, was not significantly impacted by invasive mice, ship rats and feral cats. Thus other islands within the archipelago could be prioritised for eradication programmes ahead of New Island.

**INFORMING INVASIVE SPECIES MANAGEMENT**

In addition to determining the effects of invaders, SIA can also help with formulating a response to invasions. By understanding the food used and locations from which it has been obtained, behavioural patterns can be identified that enhance the chances of successfully eliminating a population. An example of this approach was proved for invasive American mink (*Neovison vison*) in the Outer Hebrides, UK (Bodey et al. 2010). Stable isotopes can also help shape eradication protocols alongside a suite of standard techniques. For example, the likely outcomes of species eradication such as the disruption of trophic interactions, or the ecological release of other species, can be assessed more thoroughly prior to any eradication attempt as was carried out on a whole island basis prior to ship rat removal from Surprise Island, New Caledonia (Caut et al. 2009).

The logistics of eradicating common invasive mammals from small islands are now well understood. Successful eradications have continued to increase in size and complexity (Towns and Broome 2003; Vezich et al. 2011). However, increases in scale are accompanied by increased risks, including a higher risk of failure from unexpected challenges. While appropriate prior planning is of course essential, an adaptive management approach (Park 2004), which seeks improvements as progress continues, is often the most effective method for tackling these risks. The extent to which detailed knowledge about a species’ ecology is required before an eradication campaign begins is debatable, particularly as the time taken to fully explore such questions may distract effort away from an efficient eradication campaign (Simberloff 2003).

Bodey et al. (2010) used SIA of diets of captured American mink early in an eradication attempt in order to reveal temporal patterns in mink behaviour that might assist the campaign. This approach identified that precise knowledge about what prey mink were consuming or when it was consumed was not necessary. Instead, the most useful information for the campaign was whether prey was marine or terrestrial in origin, and the relative time of consumption, coupled with background information on prey distributions. Individual variation in whicker and liver samples were used to generate a simple dietary time series. This revealed the continual importance of marine food sources to the population as a whole while the eradication progressed. Intra-sexual and intra-island differences were also found, and this again demonstrated that combining SIA with knowledge of prey distributions and gut analysis was crucial. For example, the presence at one locality of an additional terrestrial prey item, the introduced field vole (*Microtus agrestis*), is likely to have contributed to different behavioural patterns.

The use of SIA to inform eradication campaigns could greatly benefit invasive species management by revealing local areas of foraging, habitats or areas in which animals may concentrate their time, and plasticity of responses to different trophic webs. The technique can help to refine methodologies and protocols, highlight areas for trap placement and assist with focussing of resources, potentially creating ecological traps for the target species.

**CAVEATS AND CONCLUSIONS**

Stable isotope analyses have transformed our understanding of numerous ecological questions about native species. There is a natural progression from these to its use for quantifying and resolving the effects of invasive species, and then to inform eradication campaigns. Unsurprisingly though, the use of SIA comes with some caveats. For example, there may be difficulties with interpreting the origins of food from multiple sources, variation in assimilation rates of isotopes into tissues both between individuals and species, and resolving the output of complicated statistical models (Crawford et al. 2008; Inger et al. 2008; Kurle 2009). Furthermore, additional work is required if we are to advance our understanding of turnover rates and growth times of specific animal tissues. On the other hand, while such information may be interesting, it may be beyond the information needed for an eradication programme. Thus, the few complexities with interpretation are not sufficient to prevent the incorporation of stable isotopes into management programmes. Given the value of adaptive management for the control or eradication of invasive species, SIA provides an additional tool with considerable potential to inform management options.

When combined with other methods, SIA can maximise the information obtained from culled individuals, enable rapid data accumulation, and thus inform areas of uncertainty as quickly as possible. Furthermore, it can aid preliminary studies on the feasibility of eradications, inform operations as they progress, and inform models of potential outcomes. Additionally, collection of samples such as fur, feathers and blood for SIA can be through non-lethal means, enabling its use to measure behavioural and dietary changes in endangered species pre- and post-eradication. Stable isotopes may also shed light on subsequent restoration attempts. For example, Gratton and Denno (2006) used changes in stable isotope values to show how disrupted trophic interactions were reconstituted after removal of the invasive *Phragmites australis* and restoration of *Spartina alterniflora* in a coastal saltmarsh. Stable isotopes can efficiently provide information at both the population and individual level from relatively small samples on species that may otherwise be difficult to study. They can be used to examine behavioural and ecological changes, and to describe the dietary and habitat plasticity of invasive species. They thus have great potential to inform management options, and should be seen as a powerful addition to the eradication toolkit.
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REFERENCES


