Individual specialists in a generalist population: results from a long-term stable isotope series

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Individual variation in resource use has often been ignored in ecological studies, but closer examination of individual patterns through time may reveal significant intrapopulation differences. Adult loggerhead sea turtles (*Caretta caretta*) are generalist carnivores with a wide geographical range, resulting in a broad isotopic niche. We microsampled scute, a persistent and continuously growing tissue, to examine long-term variation in resource use (up to 12 years) in 15 nesting loggerhead turtles. Using stable isotopes of nitrogen and carbon, we examined the resource use patterns (integration of diet, habitat and geographical location) and demonstrate that individual loggerheads are long-term specialists within a generalist population. We present our results in the context of a conceptual model comparing isotopic niches in specialist and generalist populations. Individual consistency may have important ecological, evolutionary and conservation consequences, such as the reduction of intraspecific competition.

Keywords: isotopic niche; resource use; sea turtles; specialist; stable isotopes

1. INTRODUCTION

Hutchinson's (1957) conceptualization of the niche as an *n*-dimensional hypervolume of resource use has since been expanded in the ecological literature. Van Valen (1965) first incorporated the idea of individual variation in resource use into niche theory, but intrapopulation variation in resource use is often overlooked in ecological studies (Bolnick *et al.* 2003). While there are many niche concepts based on various ecological characteristics, a recent expansion of the niche theory uses stable isotopes as the measure of niche width (Bearhop *et al.* 2004; Newsome *et al.* 2007). Examining intra- and inter-individual isotopic variance can be an effective way to investigate specialization and the ecological niche (Newsome *et al.* 2007; but see Matthews & Mazumder 2004).

Stable isotopes of consumers reflect that of prey as well as the habitat of the individual. Nitrogen isotopes typically indicate trophic position (Post 2002), while carbon isotopes reflect variation in baseline producers

or habitat (DeNiro & Epstein 1978). Tissues that are created over time and remain inert after synthesis, such as hair, otoliths and baleen, reflect resource use at the time of formation (Hobson 1999) and allow longitudinal sampling with stable isotope analysis of successive microlayers (Cerling *et al.* 2009; Cherel *et al.* 2009). Sea turtles have such a tissue—scute—which is a keratinized epidermis covering the bony shell of most chelonians. Scute grows from basal epidermis and accumulates with the oldest tissue at the surface, making possible the examination of resource use (which we define here as the integration of diet, habitat and geographical location) of individuals over time.

Figure 1 presents a conceptual model of the isotopic records from an inert tissue of three hypothetical time series of resource use for one specialist and two generalist populations. In our model, isotopic signatures may be influenced by diet, habitat type and geographical location. We use specialization to refer to the use of a relatively limited fraction of the possible range of available resources. In the specialist population (figure 1*a*), both individual and population isotopic niche widths are narrow. In the first generalist population (figure 1*b*), generalist individuals vary widely in their resource use, resulting in an isotopic record that shifts through time so that both individuals and the population occupy a wide isotopic niche space. In the second generalist population (figure 1*c*), specialist individuals maintain consistent resource use within a narrow isotopic niche space, but variation among individuals results in a wide population isotopic niche. Without long-term individual records, the generalist populations in figure 1*b,c* are indistinguishable. As drawn, our conceptual model assumes no temporal variation. However, the horizontal lines in figure 1*a,c* would exhibit a cyclic pattern if seasonal variation occurred. Our model does not address asynchronous temporal variation among sites.

The endangered loggerhead sea turtle (*Caretta caretta*) is a generalist species that feeds on a wide range of prey (Bjorndal 1997). Loggerheads nesting in Florida forage over a broad geographical range from New Jersey, USA, to Belize, and these geographical areas have different isotopic baselines (Reich *et al.* 2010). We examine the long-term consistency in resource use of a nesting loggerhead population through stable isotope analysis of $\delta^{15}N$ and $\delta^{13}C$ in scute layers to distinguish between the two types of generalist populations. Given the generalist nature at the population level, our objective is to reveal the individual patterns of resource use in loggerheads—that is, do individuals forage over a broad resource base or are they specialists within the generalist population?

2. MATERIAL AND METHODS

Scute samples were taken with sterile 6 mm biopsy punches from 15 adult female loggerheads (curved carapace length range 86.5–108.8 cm) while nesting at Cape Canaveral National Seashore, FL, USA, in May–June 2004. After lipid extraction with petroleum ether using an accelerated solvent extractor, scutes were microsampled in 50 µm layers to provide a sufficient sample for stable isotope analysis using a carbide end mill with *x*, *y* and *z* axes controls to a precision of 10 µm. The number of 50 µm layers in a sample ranged from 8 to 22.

We analysed variation in $\delta^{15}N$ and $\delta^{13}C$ using multivariate analysis of variance (MANOVA) with the Wilks' lambda test. We then
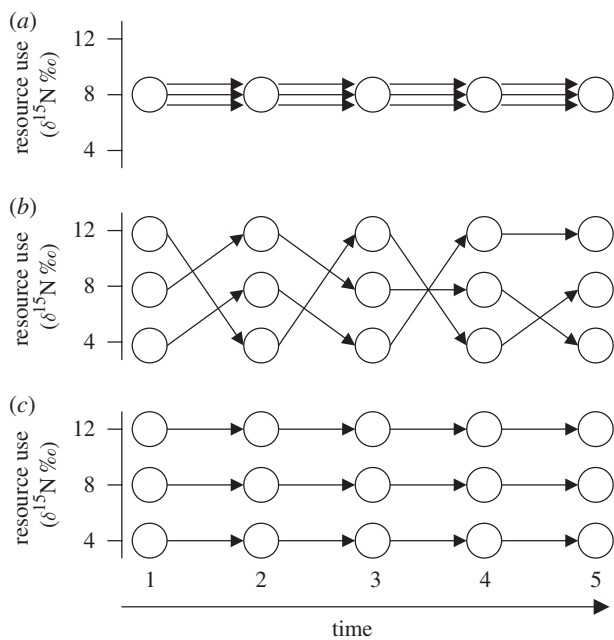
Figure 1. Conceptual model of three population patterns of isotope signatures representing resource use through time. Arrows track individuals, and each circle represents the $\delta^{15}N$ value for a layer of inert tissue, which reflects resource use (integration of diet, habitat and geographical location). See text for discussion of the three strategies. (a) Specialist population–specialist individuals; (b) generalist population–generalist individuals and (c) generalist population–specialist individuals.

used protected analysis of variances (ANOVAs) to compare variation in $\delta^{15}N$ or $\delta^{13}C$ within and among turtles.

We estimated the time required for scute to grow 50 μm to calculate the duration represented in an entire scute sample. First, we adjusted the known rate of isotopic incorporation of scute in growing juvenile loggerheads (Reich *et al.* 2008) to non-growing adults. Using the adjusted incorporation rate, we estimated the complete turnover as four half-lives, which is the time a new isotopic equilibrium would be reached after a shift in resource use. We applied this to an apparent shift in the $\delta^{13}C$ signature of one individual that occurred over several layers (open circle in figure 2b; figure S1 in electronic supplementary material). See electronic supplementary material for detailed methods.

3. RESULTS

We estimated that one 50 μm layer of loggerhead scute is equivalent to 0.6 years. The scute samples range from 400 to 1100 μm in depth, and thus, the time interval in the entire scute record ranges from 4 to 12 years (median 8).

Individuals exhibit high consistency in both $\delta^{15}N$ and $\delta^{13}C$ (figure 2), and the mean range of individuals is much smaller than that of the population for nitrogen and carbon (table 1). Individual patterns in resource use in both $\delta^{15}N$ and $\delta^{13}C$ combined (figure S2 in electronic supplementary material) reveal individual consistency (MANOVA, $F = 437$, $p < 0.001$). Based on ANOVAs, variation within individuals (less than 7% of total variation) was less than that among individuals (table 2).

4. DISCUSSION

We estimate that loggerhead scute samples may contain up to 12 years of resource use history, providing a lengthy record from which to investigate patterns in
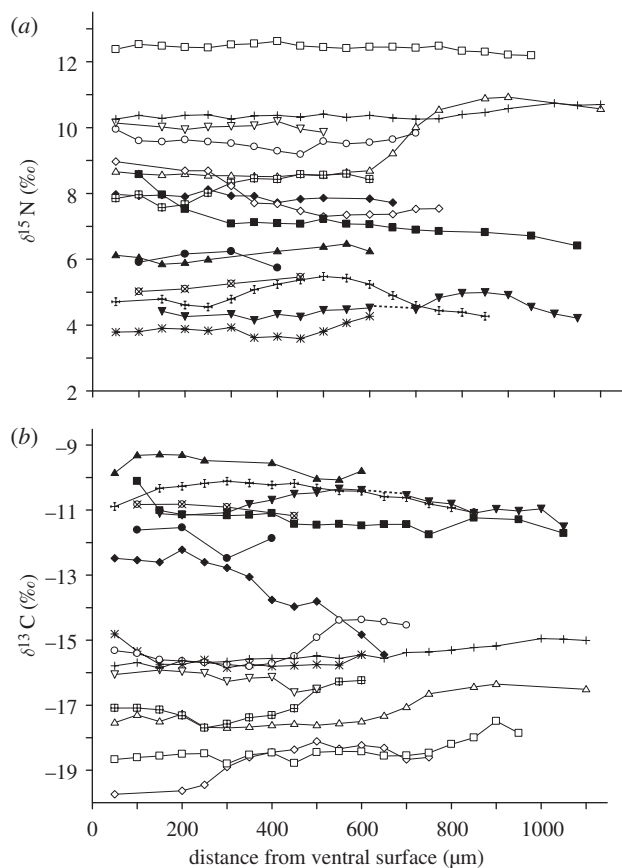
Figure 2. (a) $\delta^{15}N$ values of successive scute layers from 15 loggerheads. Each line represents all layers for one individual, noted with a unique symbol. (b) $\delta^{13}C$ values with the same format and the same individual symbols as (a). Starting points and intervals vary for some individuals because layers were combined to provide sufficient samples for analysis. The number of layers reflects the thickness of the sample.

Table 1. Minimum, maximum and mean ranges of $\delta^{15}N$ and $\delta^{13}C$ for individual scute records ($n = 15$). (The population range is the difference between the maximum and minimum values for all individuals.)

	minimum range (‰)	maximum range (‰)	mean range (±s.d.) (‰)	population range (‰)
$\delta^{15}N$	0.33	2.42	0.93 (±0.66)	9.03
$\delta^{13}C$	0.36	3.23	1.26 (±0.65)	10.45

a long-lived species. To our knowledge, our study reports the longest record of resource use history obtained from living individuals.

Comparison of long-term scute records (figure 2) with isotopic scenarios presented in figure 1 reveals that this generalist population is composed of individual specialists. Although all of these loggerheads were sampled at the same nesting beach and an entire ocean basin is potentially available to the population, individuals use only a limited fraction of the available isotopic niche space (figure S2 in the electronic supplementary material).

In our study, specialization is not limited to a diet consisting of a single prey item, but the observed specialization results from a consistent mixture of

Table 2. ANOVAs indicate significant differences between the means of individuals, with a large proportion of the variation attributed to among rather than within individuals.

	SS-among	SS-within	F	p-value
$\delta^{15}N$	1251.7	89.4	533.2	<0.001
$\delta^{13}C$	1767.8	36.6	623.3	<0.001

prey, habitat and geographical location, which we are unable to separate with our sampling regime. Consumption of a prey mixture is likely, as individual loggerhead stomach contents often contain several prey species (Bjorndal 1997). While some of the variation among individuals may be owing to individual variation in isotopic discrimination or physiology rather than differences in foraging (Barnes *et al.* 2008), it is unlikely that this would result in the wide isotopic range observed.

The large population range in $\delta^{15}N$ values (9.0‰) could be indicative of a population that is feeding over several trophic levels if the baseline nitrogen is stable in all of the foraging locations of these individuals (Post 2002). However, if baseline nitrogen signatures change with foraging location, isotopic differences will be more reflective of habitat or location than of trophic level feeding differences because the same prey species will have different isotope signatures among these areas. We believe locational differences are more likely than trophic level differences, as the similarly large range of $\delta^{13}C$ values (10.5‰) indicates that loggerheads have geographically separated foraging areas and/or are incorporated in food webs with enriched or depleted $\delta^{13}C$ producers.

The gap in $\delta^{13}C$ values between -12.5‰ and -14.5‰ (figure 2*b*) represents the division between two foraging groups identified by Reich *et al.* (2010). The groups represent two general habitat use patterns that could result from food webs with different $\delta^{13}C$ baselines owing to an isotopic gradient (e.g. oceanic/neritic, pelagic/benthic, latitudinal). Only one turtle crossed between groups, indicating that individuals have high fidelity to foraging sites and/or habitat type. This foraging fidelity is consistent with the observations of eight adult female loggerheads tracked from North Carolina, USA; two different movement types were observed, but all individuals exhibited interannual fidelity to discrete foraging sites (Hawkes *et al.* 2007).

Intrapopulation variation in resource use can have ecological, evolutionary and conservation consequences. Resource use heterogeneity, indicated by the broad population isotopic niche width and narrow individual niche widths, reduces intraspecific competition and may alter selective pressures (Bolnick *et al.* 2003). Reduction in intraspecific competition appears to be substantial in adult loggerheads, given the small proportion of variance in our study attributed to within-individual variation (less than 7%, table 1). In comparison, a recent study of diet specialization in sea otters, based on vibrissae isotope signatures, estimated that 28 per cent of the variance was attributed to within-individual variation (Newsome *et al.* 2009).

Examining the degree of individual specialization within a population provides a better understanding of its ecology, behaviour and population dynamics. Our approach to resource use has broad application for species that possess consistently growing, inert tissues that can be serially sampled. Because diet and habitat are confounded in this study, loggerheads should be sampled at a series of foraging grounds to distinguish the effects of diet, habitat and geographical location on isotopic signatures.

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