

TECHNICAL COMMENT

Isotopic niche is not equal to trophic niche

Nicolas Hette-Tronquart*

Irstea UR RECOVER Aix-en-Provence, France

*Correspondence: E-mail: nicolas.hette@edu.mnhn.fr

Abstract

The work of Sheppard *et al.* (Ecol. Lett., 21, 2018, 1395) relies on the strong assumption that isotopic niche is equal to trophic niche. Here I raise three main concerns showing that classic hypotheses built upon trophic niche cannot be directly interpreted in isotopic space. Future studies should always keep isotopic and trophic niches distinct.

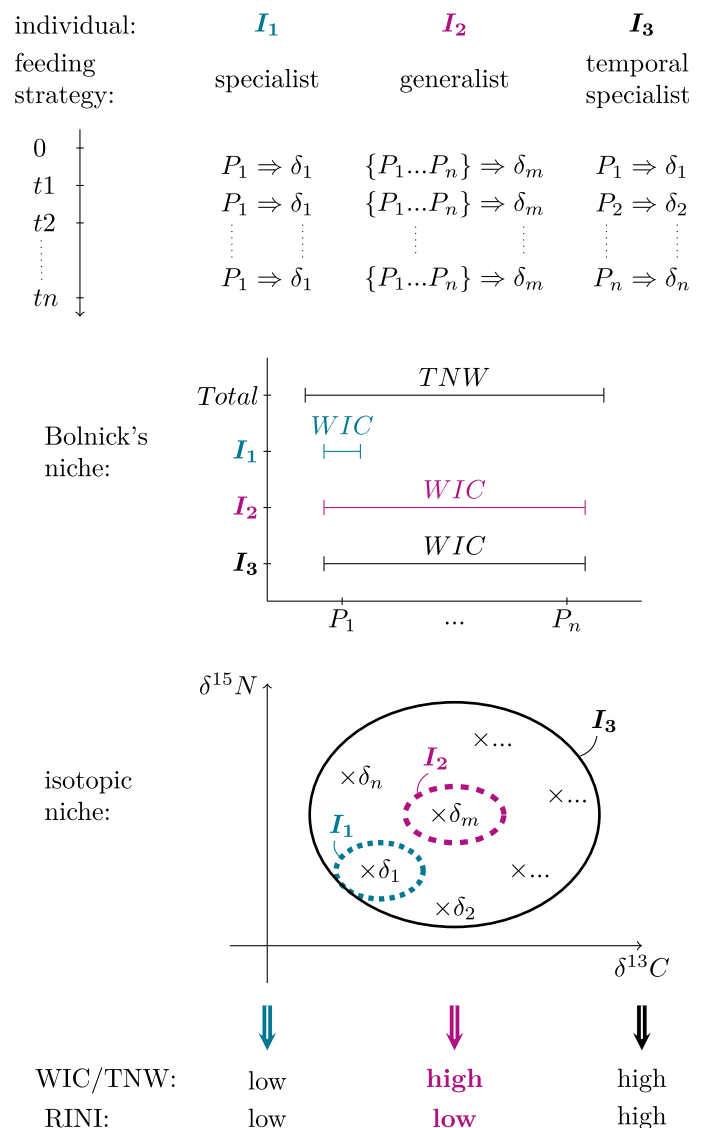
Keywords

Feeding strategy, intragroup competition, isotopic space, niche overlap, niche partitioning, stable isotope, trophic space.

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Sheppard *et al.* (2018) examined the effect of intragroup competition on individual feeding strategies of mongooses. Competition was assessed using the number of individuals within a group, and feeding strategy was evaluated by a relative individual niche index (RINI, defined as a ratio of individual to group isotopic niches) via stable isotope analysis. The authors concluded that higher intragroup competition led to individual foraging specialisation. Here I raise three main concerns about this interesting study, illustrating why it is essential to make a difference between trophic and isotopic spaces.

Figure 1 Three typical feeding strategies and their meaning in terms of stable isotopes at the different sampling times (t_i). The comparison with the traditional approach of Bolnick *et al.* (2003) highlights the first limitation of the RINI metric. In Bolnick's approach TNW is the group's total niche, WIC is the within-individual component of the group's niche, and the ratio WIC/TNW provides a measure of individual specialisation. The first feeding strategy is displayed by individual I_1 , always specialising on the same prey P_1 . Thus, the isotopic signal of I_1 does not change over time and reflects that of P_1 (δ_1). Individual I_2 is generalist, always feeding on the same mixture of prey $\{P_1 \dots P_n\}$. As a result, the isotopic signal of I_2 does not change either and averages those of its prey (δ_m). Over time, individual I_3 is also generalist and feeds on the same mixture of prey as I_2 , but the feeding strategy is quite different. At each time t_i , I_3 is changing its diet and specialising on a different prey (P_i). The isotopic signal follows the diet and changes over time (δ_1 at $t_1 \dots \delta_n$ at t_n). According to Bolnick's approach, the individual niche of I_1 (WIC) is small, centred on P_1 , while the niches of I_2 and I_3 are large, covering the whole range of available prey. The trophic niche of the group is given by TNW. In the isotopic space, the niches of I_1 and I_2 are relatively small, whereas that of I_3 is large. The group's isotopic niche approximates that of I_3 . Following the WIC/TNW approach of Bolnick *et al.* (2003), Sheppard *et al.* (2018) defined the RINI as the ratio of individual to group niche size in the isotopic space. Yet, the two approaches lead to distinct results. For I_2 , WIC/TNW is high, while the value of RINI is low. Most importantly, the RINI values of I_1 and I_2 are similarly low, whereas that of I_3 is high. This shows that the RINI cannot discriminate any kinds of feeding strategies (from specialist to generalist), when the strategy does not change over time. More likely, the RINI reflects the variability in diet over time, with low values indicating stability.



FEEDING STRATEGY AND STABLE ISOTOPES

Stable isotopes integrate diet over time (Vander Zanden & Rasmussen 1999). As a consequence a generalist feeding strategy, represented by several resources in the trophic space, is only represented by one point in the isotopic space. In mathematical words, the function relating trophic and isotopic spaces is surjective, which implies that topological hypotheses in the trophic space cannot be directly interpreted in the isotopic space. The RINI of Sheppard *et al.* (2018) provides a good illustration of this issue. By analogy with classic metrics of the trophic space (e.g. WIC/TNW, where TNW is the group's total niche width that includes a within-individual component WIC, Bolnick *et al.* 2003), the authors assumed that a generalist feeding strategy leads to a large isotopic niche and a high RINI. However, a large niche in the trophic space is not necessarily displayed by a large isotopic niche. Indeed, when diet does not change over time, the isotope signals do not change either, resulting in a small isotopic niche and a low RINI value regardless of the feeding strategy (Fig. 1). Consequently, the RINI cannot be interpreted in terms of foraging specialisation, but only reflects the variability in diet over the sampling period, in the best case.

MEANING OF ISOTOPIC VARIABILITY

Most of the time variability in isotope signals not only reflects the variability in diet (Yeakel *et al.* 2016), but also integrates both the variability in the isotopic baseline and the variability in the diet-tissue discrimination factor (Δ , Post 2002). Considering both sources of variability is thus essential to assess the variability in diet from isotopic variability. The study of Sheppard *et al.* (2018) is no exception to this rule. First, variation in the isotopic baseline is likely to occur due to the sampling design and the feeding habits of mongooses. Typical prey of mongooses are invertebrates (Rood 1975), whose isotopic signals have been reported (e.g. De Visser *et al.* 2008) to vary over shorter time-frame, or smaller spatial scale, than the ones considered in the mongoose study. Although the isotopic variability in invertebrates is not expected to covary with mongoose group size, further information is required to discard this potential source of variability. Moreover, variability in the diet-tissue discrimination factor is particularly relevant in Sheppard *et al.* (2018). Among the drivers of discrimination factor, growth rate, for example is known to covary with competition (Jenkins *et al.* 1999) and can lead to higher isotopic variability (Δ 1.8–3.6, Gorokhova 2018) than the individual variability observed by Sheppard *et al.* (2018) for mongooses (1.0 ± 0.6 ‰ for $\delta^{15}\text{N}$, mean \pm SD, see Calculations S1 in Supporting Information). Thus, this source of variability could reduce the strength of the relationship observed in the mongooses.

NICHE OVERLAP IN THE ISOTOPIC SPACE

The relationship between isotopic niche and niche overlap is not straightforward. Mathematically, mean size of the individual isotopic niche, even expressed as the proportion of the group's niche, is not sufficient to deduce the degree of overlap (e.g. Fig. 2a). Defining the degree of overlap also requires

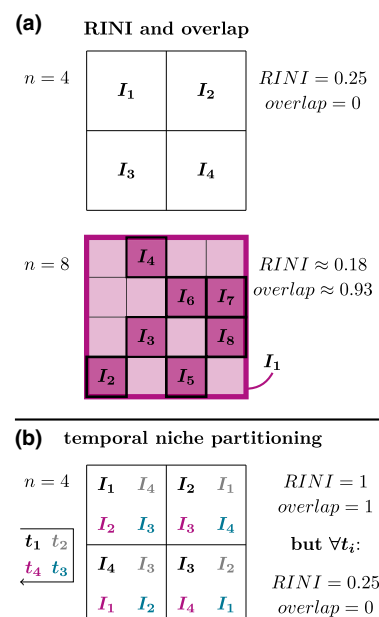


Figure 2 Interpretation of RINI in terms of niche partitioning. Here, isotopic niches are displayed as squares for easy interpretation. I calculated niche overlap as the proportion of an individual niche occupied by the other group members (see Calculations S1). (a) Isotopic niches of two groups differing by their number of individuals. In the first case ($n = 4$), the four individuals are feeding on four different niches of same size (1/4 of the group niche), resulting in a RINI of 0.25 and no overlap. In the second case ($n = 8$), the niche of individual I_1 covers the niche of the entire group. The other seven individuals display smaller niches (1/16 of the group niche) that overlap with the niche of I_1 . On average, the RINI of the group is 0.18, smaller than the previous group, whereas the overlap is largely higher (0.93). It is worth noting that this theoretical example mirrors the real cases observed by Sheppard *et al.* (2018) quite well. On their Fig. 4a, the three groups with the lowest RINI values (groups with 25–30 individuals) are very like the group in the present figure with eight individuals. For example the group in Sheppard *et al.* (2018) with 25 individuals displays one individual with a very high RINI value (0.89), while other group members have low RINI values (< 0.4). In such groups, the individual displaying a large RINI could be dominant, restraining the others to small RINIs. (b) Temporal niche partitioning for a group with four individuals. Over the whole sampling period (from t_1 to t_4), the four individuals occupy the same isotopic niche (the great square), and it seems that the niches overlap completely. In reality, the individuals are not in the same isotopic place at the same time. At each time t_i , each individual occupies a different quarter of the whole niche, and the individual niches are completely segregated.

examining how isotopic niche size is distributed in the group. Within the mongoose study, the three groups with the lowest RINI values (groups with 25–30 individuals in Figure 4a of Sheppard *et al.* 2018) display a peculiar RINI distribution: all individuals but one have low RINI values. The group with eight individuals proposed in Fig. 2a mimics this distribution and shows that such groups could display a high degree of overlap despite showing low RINI values. It is thus not possible to interpret the data in Sheppard *et al.* (2018) in terms of niche partitioning. In addition, apparent overlap among niches could hide a real temporal niche partitioning (Fig. 2b). An appropriate time-frame is thus of critical importance in identifying niche overlap (Kernaléguen *et al.* 2016). For instance, Sheppard *et al.* (2018) calculated the RINI over a

long period of 663 days on average. As a result, the RINI cannot be used to assess daily or even monthly competition.

CONCLUSION

Such concrete examples illustrate how trophic and isotopic spaces differ. Three points are of critical importance for future ecological studies: (1) the interpretation of stable isotope signals in terms of feeding strategy, (2) the meaning of isotopic variability and (3) the assessment of niche overlap in isotopic space. I hope these comments will raise the awareness of such concerns in the scientific community.

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AUTHORSHIP

NHT performed the review, the analyses and wrote the manuscript.

DATA ACCESSIBILITY STATEMENT

Not relevant in the case of this technical comment.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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