



Stable isotopes are quantitative indicators of trophic niche

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Stable isotopes are quantitative indicators of trophic niche

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9
10 26 other than the data associated with the original paper (Sheppard et al. 2018) that is already publicly
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12 27 available.
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37 **Abstract**

38 Hette-Tronquart (2019) raises three concerns about our interpretation of stable isotope data in
39 Sheppard et al. (2018). We feel that these concerns are based on comparisons that are unreasonable
40 or ignore the ecological context from which the data were collected. Stable isotope ratios provide a
41 quantitative indication of, rather than being exactly equivalent to, trophic niche.

For Review Only

42 Introduction

43 Hette-Tronquart (2019) raises three concerns about our study demonstrating that increased
44 intragroup competition predicts higher individual foraging specialisation in banded mongooses
45 *Mungos mungo* (Sheppard *et al.*2018). We address each of these concerns in turn using the same
46 sub-headings as Hette-Tronquart.

47 Feeding strategy and stable isotopes

48 Hette-Tronquart highlights that stable isotope measures integrate dietary information over the time
49 period which the analysed tissue was synthesised (sampling period). Therefore, the multiple stable
50 isotope values used to create our relative individual niche index (RINI) measure “the variability of
51 diet over the sampling period” and so we may not be able to differentiate between feeding
52 strategies that vary over shorter or longer timescales than the sampling period. We recognised this
53 in our study and acknowledge again that when interpreting the ecological meaning of stable isotope
54 data, it is fundamental to consider this sampling period (Bearhop *et al.*2004). In our study, $^{13}\text{C}:^{12}\text{C}$
55 and $^{15}\text{N}:^{14}\text{N}$ isotope ratios were measured from mongoose vibrissae that had a mean growth time of
56 6.3 months (lower-upper s.e.=5.3–7.8, Sheppard *et al.*2018). Rainfall at our study site, which drives
57 invertebrate prey abundance, fluctuates seasonally every 2-5 months (Marshall *et al.*2017). As such,
58 the tissues we used to calculate each RINI value indicate between-season variation in individual diets
59 (noting the influence of others factors below).

60 The timescale over which stable isotope data are measured may influence the foraging
61 strategy they suggest. For example, one individual might always have a narrow diet but regularly
62 switch prey items between time periods (e.g.seasons). Another individual may maintain a broader
63 diet across these time periods that incorporates a wider range of prey items than the first individual
64 at any given time point but not the full range of prey consumed by the first individual across all
65 periods. Here, the first individual may appear more “specialist” within a time period but more
66 “generalist” across time periods. Selection of the sampling period depends on the individual

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3 67 researcher judging what is ecologically relevant and what tissues are feasibly available. Future work
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5 68 exploring this relationship between sampling period and foraging strategy would provide valuable
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7 69 insights in foraging niche ecology and more broadly, the ecology and evolution of between-
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9 70 individual differences in behavioural plasticity (Nussey *et al.* 2007; Dingemanse & Wolf 2013).
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71 **Meaning of isotopic variability**

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15 72 Hette-Tronquart suggests that the variation we observed in mongoose stable isotope ratios may be
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17 73 due to temporal changes in prey isotope values ('isotopic baseline') rather than variation in
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19 74 individual diet (Yeakel *et al.* 2016). However, as he points out, there is no reason to expect the
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21 75 isotopic baseline to vary systematically with mongoose group size (our measure of intragroup
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23 76 competition). This potential source of bias is, therefore, unlikely to have influenced our findings.
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27 77 Hette-Tronquart also suggest that our findings may be due to individual differences in
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29 78 discrimination factors since these can be affected by growth rates (Jenkins *et al.* 1999), which in turn
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31 79 can be influenced by competition (Gorokhova 2018). This argument is based on variation in nitrogen
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33 80 discrimination factors from different experimental growth rates (Gorokhova 2018) being larger than
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35 81 the variability in $\delta^{15}\text{N}$ that Hette-Tronquart calculates from our data. The values in Gorokhova (2018)
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37 82 were measured in sub-adult marine shrimp (*Neomysis integer*) under laboratory feeding regimes
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39 83 (including total starvation). It is not reasonable to apply this observation to physiological processes
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41 84 in a wild population of, predominantly adult, mammals (mean \pm s.d. = 3.5 \pm 1.6 years, n=64, Sheppard *et*
42
43 85 al. 2018) subject to seasonal, but not extreme (e.g. starvation), changes in food availability. In
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45 86 addition, the $\delta^{15}\text{N}$ variability measures calculated by Hette-Tronquart include mongooses with three
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47 87 or fewer isotope values which were excluded from our analyses. Repeating these calculations using
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49 88 the 64 individuals with four or more values produces a mean \pm s.d. $\delta^{15}\text{N}$ of 1.4 \pm 0.5 rather than
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51 89 1.0 \pm 0.6.
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3 **91 Niche overlap in isotopic space**
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6 92 Hette-Tronquart's final concern is that individual foraging niche sizes within a social group are not
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8 93 informative about the degree of niche overlap. Whilst we expect a relationship between niche size
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10 94 and overlap, any ecological relationship between two variables is certain to contain a non-trivial
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12 95 amount of variation caused by other factors. This is especially so when considering indirect
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14 96 measures of ecological processes. Stable isotope values are influenced by consumers' diets but also
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16 97 by their habitat use and tissue synthesis processes. We argue that where two variables are
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18 98 correlated they can still provide useful information about each other as long as other sources of
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20 99 variation are acknowledged.
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24 100 Second, the two panels in Hette-Tronquart's figure 2a used to illustrate his argument are not
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26 101 comparable as they contain different numbers number of individuals (4 vs 8). If both include 8
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28 102 individuals then $RINI=0.125$ and 0.18 , respectively (rather than 0.25 and 0.18 ; see fig.1). We included
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30 103 the proportion of individuals sampled in our models to control for this sample size effect. Hette-
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32 104 Tronquart also calculates overlap as the mean area that each individual's niche overlaps with any
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34 105 other. This definition of overlap considers whether competition is occurring at a given point in niche
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36 106 space but not the intensity of this competition (i.e. the number of competitors). As such, in the
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38 107 second panel of Hette-Tronquart's figure 2a individuals I_{2-8} can have niches up to 7 times larger
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40 108 without affecting the mean overlap, as long as these niches expand into space that is already
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42 109 occupied. This assumes that once two individuals' niches overlap at a particular point in niche space,
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44 110 a third individual's niche at this point has a negligible effect on competition. We argue that the
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46 111 proportion of group members that an individual is competing with (signified by individuals' niches
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48 112 overlapping) would be a more ecologically relevant measure of competition. In the scenario
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50 113 presented by Hette-Tronquart this more relevant measure produces mean overlap values of 0 and
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52 114 0.25 rather than 0 and 0.93 (fig.1).
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3 115 Finally, we restate here our agreement that considering the timescale over which stable isotope
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5 116 data is sampled is important in their interpretation, and that our study cannot test for temporal
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7 117 niche partitioning. However, the RINI would support assessment of niche variation over shorter
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9 118 timescales (e.g.days) if the measures were based on tissue samples synthesised over shorter
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12 119 periods.

15 120 **Conclusion**

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18 121 These discussions emphasise the importance of considering tissue synthesis time and ecological
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20 122 relevance when analysing and interpreting stable isotope data. Stable isotope data are influenced by
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22 123 consumers' diets, but also the habitats they occupy and their tissue synthesis processes.
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24 124 Consideration of all of these sources of variation is important when interpreting stable isotope
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26 125 values since, rather than being directly equivalent, they provide a quantitative indicator of trophic
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28 126 niche.

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35 128 **Acknowledgements**

37
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40 130 reviewers for constructive criticism of the original version of this response.

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37 154 **Figure legends**

38
39 155 Figure 1: Redrawing Hette-Tronquart's figure 2A. Isotopic niches of individuals (I_{1-8}) within a social
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41 156 group showing the mean relative individual niche index (RINI) and niche overlap in each scenario.
42
43 157 Hette-Tronquart's two panels in his figure 2A contain different numbers of individuals (4 vs 8). Here,
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45 158 panel (a) corrects the scenario containing four individuals to contain eight, making this comparable
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47 159 with panel (b). Hette-Tronquart calculates overlap as the mean proportion of each individual's niche
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49 160 occupied by another group member. Here, panels (a) and (b) show how the overlap values change
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51 161 when this is calculated using the proportion of other group members with which each individual's
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53 162 niche overlaps.
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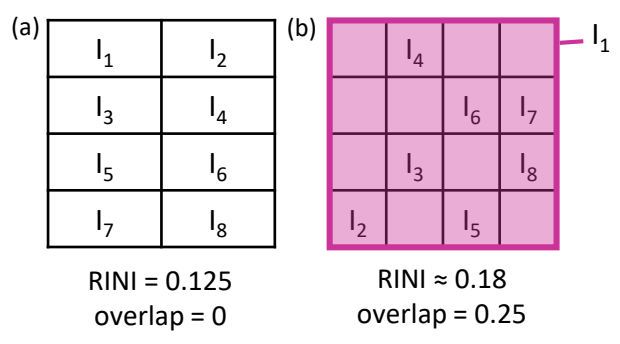


Figure 1