An experimental framework for quantifying the degree of intraguild predation in a three-species omnivorous food web in the fieldd

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Abstract:	1. Intraguild predation (IGP) is common in natural and human-managed systems and plays a critical role in food web dynamics. Although studies have documented the occurrence of IGP across a wide range of predator taxa, quantitative understanding regarding the degree/intensity of IGP remains lacking. 2. I propose an experimental framework combining controlled feeding trials and stable isotope analysis to quantify the degree of IGP in a three-species omnivorous food web (top predator + mesopredator + shared prey) in the field. The degree of IGP is defined as the proportion (in number) of mesopredator consumed in the total diet (shared prey + mesopredator) of the top predator. 3. Feeding trials along with stable isotope analysis are used to construct a standard curve of the relationship between top predator's diet and shift in its nitrogen isotope signatures. The nitrogen isotope signatures of field-sampled top predator individuals are then analyzed and interpolated to the curve to estimate the degree of IGP in the field. 4. The proposed framework leverages the strengths of different experimental approaches to studying trophic interactions, providing a practical tool for quantifying IGP in a more accurate (controlled feeding trials and standard IGP curve) and realistic (stable isotope analysis of field samples) fashion. The current framework can be further extended to food webs involving more complex interactions (e.g., cannibalism and multiple shared prey) and complemented with other approaches (e.g., molecular gut content analysis) to capture a more complete picture of IGP dynamics in the field.

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1   **Title**

2   An experimental framework for quantifying the degree of intraguild predation in a three-

3   species omnivorous food web in the field

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16   **Running headline**

17   Framework quantifying intraguild predation

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1

19   **Abstract**

20   1.   Intraguild predation (IGP) is common in natural and human-managed systems and plays

21   a critical role in food web dynamics. Although studies have documented the occurrence

22   of IGP across a wide range of predator taxa, quantitative understanding regarding the

23   degree/intensity of IGP remains lacking.

24   2.   I propose an experimental framework combining controlled feeding trials and stable

25   isotope analysis to quantify the degree of IGP in a three-species omnivorous food web

26   (top predator + mesopredator + shared prey) in the field. The degree of IGP is defined as

27   the proportion (in number) of mesopredator consumed in the total diet (shared prey +

28   mesopredator) of the top predator.

29   3.   Feeding trials along with stable isotope analysis are used to construct a standard curve of

30   the relationship between top predator's diet and shift in its nitrogen isotope signatures.

31   The nitrogen isotope signatures of field-sampled top predator individuals are then

32   analyzed and interpolated to the curve to estimate the degree of IGP in the field.

33   4.   The proposed framework leverages the strengths of different experimental approaches to

34   studying trophic interactions, providing a practical tool for quantifying IGP in a more

35   accurate (controlled feeding trials and standard IGP curve) and realistic (stable isotope

36   analysis of field samples) fashion. The current framework can be further extended to

37   food webs involving more complex interactions (e.g., cannibalism and multiple shared

38   prey) and complemented with other approaches (e.g., molecular gut content analysis) to

39   capture a more complete picture of IGP dynamics in the field.

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42   **Keywords**

43   feeding trial, food web, intraguild predation, mesopredator, omnivory, stable isotope analysis,

44   top predator, trophic interactions

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45   **Introduction**

46   Intraguild predation (IGP) is common in natural and human-managed ecosystems (Polis &

47   Holt, 1992; Müller & Brodeur, 2002; Arim & Marquet, 2004) and is documented across a

48   wide range of predator taxa (Polis et al., 1989; Gagnon et al., 2011). IGP could substantially

49   affect the abundance and distribution of interacting species, generating ecological and

50   evolutionary consequences for food web dynamics (Polis et al., 1989).

51   Previous studies have recorded the occurrence of IGP among arthropod predators

52   through field observations of diet compositions (e.g., Nyffeler & Sunderland, 2003; Birkhofer

53   & Wolters, 2012). Manipulative experiments in the field and laboratory have also been used

54   to examine the intensity of IGP as a function of predator and prey density (e.g., Denno et al.,

55   2004), allowing for causal inferences about the mechanisms underlying predator-predator

56   interactions and its effect on prey population. Nonetheless, the confined settings in these

57   experiments may potentially alter the encounter rates between organisms, thus leading to

58   biased results (Uiterwaal et al., 2019).

59   Stable isotopes, particularly nitrogen isotope signatures (δ^{15}N), have been used to

60   estimate the trophic levels of predators for assessing IGP (e.g., Wise et al., 2006). It is

61   suggested that IGP would increase the δ^{15}N of predators (Ponsard & Arditi, 2000). For

62   example, Rickers et al. (2006) conducted feeding experiments on wolf spiders (*Alopecosa*

63   *cuneata*) and found a higher δ^{15}N of these top predators in IGP treatment. However, the study

64   did not quantify the degree of IGP as the IGP treatment was binary (absence vs. presence of

65   mesopredator) with constant numbers of shared prey and mesopredator. On top of that, the

66   trophic levels of top predators in previous studies were often calculated based on assumed

67   trophic discrimination factors (TDFs) (Svanbäck et al., 2015). Since TDFs are often taxon-

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68   specific (Caut et al., 2009), this could lead to incorrect trophic level estimates and inferences

69   about IGP in the field.

70   Recently, researchers have applied molecular gut content analysis and immunological

71   techniques to reliably detect the presence of certain food items in predators' diet (Gagnon et

72   al., 2011), allowing for calculating the incidence rates of IGP (i.e., the percentage of top

73   predator individuals with mesopredator detected in the gut contents). Nonetheless, the

74   incidence rates may not necessarily reflect the degree of IGP in the system (Raso et al., 2014).

75   For example, it is possible that a high percentage of top predator individuals feed on

76   mesopredator yet each of them consumes on average a low proportion of mesopredator in the

77   diet. In this case, a high incidence rate of IGP only provides an incomplete picture of IGP

78   dynamics.

79   Quantifying IGP is a critical step towards a deeper understanding of food web

80   dynamics. Research has attempted to predict the intensity/degree of IGP based on allometric

81   theory (Schneider et al., 2012), yet empirical evidence remains scarce. To address this gap, I

82   propose an experimental framework combining controlled feeding trials and stable isotope

83   analysis of field samples to estimate the degree of IGP in a three-species omnivorous food

84   web (top predator + mesopredator + shared prey). The degree of IGP is defined herein as the

85   proportion (in number) of mesopredator consumed in the total diet (mesopredator + shared

86   prey) of top predator. The feeding trials will experimentally link different levels of

87   mesopredator consumption by top predator to the changes in top predator's nitrogen isotope

88   signatures via an IGP standard curve, to which the nitrogen isotope signatures of field-

89   collected top predator individuals are interpolated to estimate the degree of IGP in the field.

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92   **The proposed experimental framework**

93   The proposed experimental framework consists of three main stages: (1) first feeding trial for

94   stable isotope calibration of mesopredator and top predator, (2) second feeding trial for

95   construction of standard IGP curve, and (3) collection of field samples for IGP estimation. I

96   will illustrate the framework using an example of a terrestrial arthropod food web involving a

97   spider top predator, a spider mesopredator, and a planthopper shared prey (Fig. 1a) in the

98   following paragraphs.

99   The first feeding trial is to calibrate the nitrogen isotope signatures of the

100   mesopredator and top predator. In this trial, the two predators are fed the shared prey for a

101   period of time (Fig. 1b). The actual duration of feeding may vary depending on the species.

102   For arthropods, a period of 5–10 days will allow predators to incorporate isotope signatures

103   into their tissues and reach an isotopic equilibrium state with the shared prey (Quinby et al.,

104   2020).

105   The second feeding trial is to simulate a full range of omnivory that the top predator

106   may exhibit in the field for constructing a standard IGP curve. In this trial, the top predator is

107   fed different proportions of shared prey and mesopredator individuals from the first feeding

108   trial: (1) 100% shared prey, (2) 75% shared prey + 25% mesopredator, (3) 50% shared prey +

109   50% mesopredator, (4) 25% shared prey + 75% mesopredator, and (5) 100% mesopredator

110   (Fig. 1c). The actual numbers of shared prey and mesopredator supplied can be determined

111   based on their feeding rates, obtained through either field observations or literature. To avoid

112   the potential interfering effects of mesopredator feeding on the shared prey, the prey items

113   are presented to the top predator one at a time in a randomized sequence instead of all at once.

114   This also allows the researcher to ensure that a prey item is consumed by the top predator

115   before the next item is presented.

116   At the end of the second trial (same duration as the first feeding trial to allow for the

117   incorporation of prey isotope signatures into predator's tissues), the top predator individuals

118   in each diet treatment as well as the shared prey are prepared for stable isotope analysis to

119   obtain their $\delta^{15}N$ values. The difference in $\delta^{15}N$ between the top predator and the shared prey

120   is computed ($\delta^{15}N_{predator} - \delta^{15}N_{prey}$; experimental $\Delta^{15}N$), and a standard curve is constructed

121   by fitting a non-linear regression on the experimental $\Delta^{15}N$ against the proportion of

122   mesopredator in the diet (Fig. 1d).

123   Finally, field samples of top predator and shared prey are collected for stable isotope

124   analysis. The shared prey individuals are pooled to obtain an overall prey $\delta^{15}N$, while the

125      $\delta^{15}N$ of top predator individuals are analyzed separately and thus each predator has its own

126   empirical $\Delta^{15}N$ (i.e., $\delta^{15}N$ of each top predator individual $-$ overall prey $\delta^{15}N$). The degree of

127   IGP at the individual level can then be estimated by interpolating the individual empirical

128      $\Delta^{15}N$ to the standard IGP curve (Fig. 1e). The mean and standard error of these individual

129   IGP estimates can provide a measure of the average degree of IGP in the field and the

130   uncertainty around the mean estimate at the population level.

131   A hypothetical example of standard IGP curve construction and estimation of IGP

132   with field samples is shown in Fig. 2. In this example, five diet treatments are used; each

133   treatment contains five top predator individuals, each of which is fed 12 prey items during the

134   feeding period. After the feeding trial, the experimental $\Delta^{15}N$ of these predator individuals are

135   determined and used to construct a standard IGP curve (Fig. 2a). 20 top predator and 30

136   shared prey individuals are then collected from the field for stable isotope analysis and

137   determination of empirical $\Delta^{15}N$. An IGP estimate is calculated for each top predator

138   individual and therefore there will be a total of 20 estimates, which are further averaged to

139   quantify the degree of IGP at the population level (Fig. 2b).

140   **Applications**

141   The proposed framework leverages the strengths of different approaches to studying

142   trophic interactions—the controlled feeding trials combined with stable isotope analysis can

143   yield accurate experimental $\Delta^{15}N$ for constructing a standard IGP curve, whereas the

144   empirical $\Delta^{15}N$ derived from field samples reflects the trophic interactions under natural

145   settings. Additionally, the framework is robust to variations in background isotope signatures

146   because the IGP estimation is based on the difference in nitrogen isotope signatures ($\Delta^{15}N$)

147   rather than the original values ($\delta^{15}N$), thus allowing for comparisons across sites or systems

148   with distinct background isotope signatures.

149   The framework can be implemented along environmental gradients or under different

150   field treatments to investigate how various abiotic and biotic factors affect IGP interactions of

151   a certain food web type (e.g., arthropod food web). For instance, one can quantify and

152   compare the degree of IGP across altitudes to examine whether omnivory patterns change

153   with temperature, precipitation, or vegetation. Moreover, this study gives an example of

154   arthropod food web with spider as the top predator, but the framework applies to other

155   generalist predators as well, provided that they are amenable to feeding trials and available

156   for collection in the field.

157   Systems with clear IGP patterns and relatively simple trophic interaction networks are

158   ideal for implementing the proposed framework, as this can minimize the potential interfering

159   effects of non-focal species on the IGP interactions among focal organisms (Vance-Chalcraft

160   et al., 2007). One of such systems is agricultural system, in which IGP occurs frequently

161   (Polis et al., 1989; Rosenheim et al., 1995) and the food webs are generally less complex

162   compared with most natural ecosystems. Furthermore, understanding the degree of IGP in

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163   agricultural field can have useful implications for practitioners, for example, evaluating the

164   effectiveness of biocontrol agents in pest control programs (Müller & Brodeur, 2002).

165   A potential limitation of the proposed framework is that multiple mesopredators and

166   shared prey with different isotope signatures may exist in the field, which could introduce

167   variations into the IGP estimates for top predator individuals. The isotope signatures of top

168   predators may represent multiple dietary items over time and space. Yet, given sufficiently

169   large field samples of top predator, the average IGP estimate should fairly reflect the overall

170   IGP patterns in the field at the population level. Additionally, one can adjust the isotope

171   signatures of top predator individuals by adding an amount to (or deducting an amount from)

172   the $\delta^{15}N$ of top predator that feeds on non-focal prey with a lower (or higher) $\delta^{15}N$ than that

173   of the focal shared prey. Such calibration of $\delta^{15}N$ of top predator can yield a more accurate

174   empirical $\Delta^{15}N$ for interpolation of IGP curve.

175   A better quantitative understanding of IGP can offer critical insights into the complex

176   predator-predator-prey trophic interactions and help predict the community structure and

177   stability (Arim & Marquet, 2004; Pahl et al., 2020). I am optimistic about the practical

178   applications of the proposed framework and future experiments to validate and refine it. The

179   current framework can also be extended to food webs involving more complex interactions

180   (e.g., cannibalism and multiple shared prey) and further complemented with other approaches

181   (e.g., combining the degree of IGP at the population level with the incidence rates derived

182   from molecular gut content analysis to estimate the total IGP impact) to better elucidate the

183   IGP dynamics in the field.

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188

189   **Conflict of interest**

190   The author declares no conflict of interest regarding this manuscript.

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192   **Data accessibility statement**

193   Data archiving and sharing are not applicable to this manuscript as no new data were
194   generated or analyzed.

195

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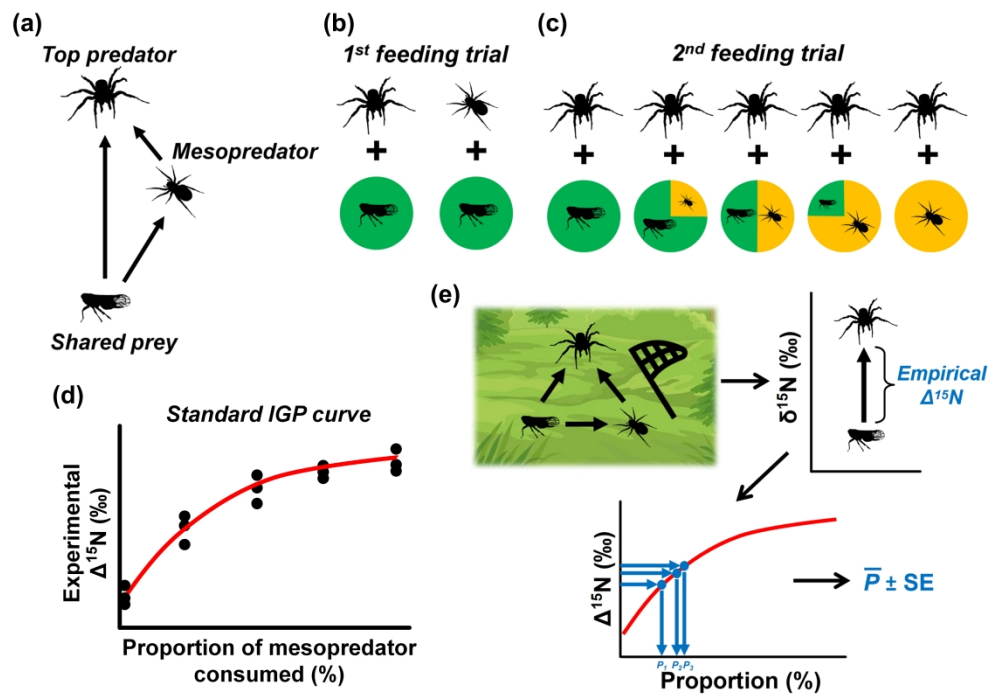
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Figure 1. A schematic diagram of the proposed experimental framework for quantifying the degree of intraguild predation (IGP) in a three-species omnivorous food web involving a spider top predator, a spider mesopredator, and a planthopper shared prey. See "The proposed experimental framework" for detailed descriptions of the steps in the framework.

645x484mm (236 x 236 DPI)

(a)

Diet treatment					
N	12/0	9/3	6/6	3/9	0/12
P	0.00	0.25	0.50	0.75	1.00
Δ¹⁵N (‰)	1.0	1.4	2.2	2.4	2.9
	0.8	1.8	2.1	2.4	2.7
	0.9	1.3	1.7	2.3	2.7
	0.9	1.5	2.2	2.5	2.6
	1.0	1.5	2.0	2.3	2.8

(b)

$n_{predator} = 20$

$n_{prey} = 30$
(pooled $\delta^{15}N = 2.0$)

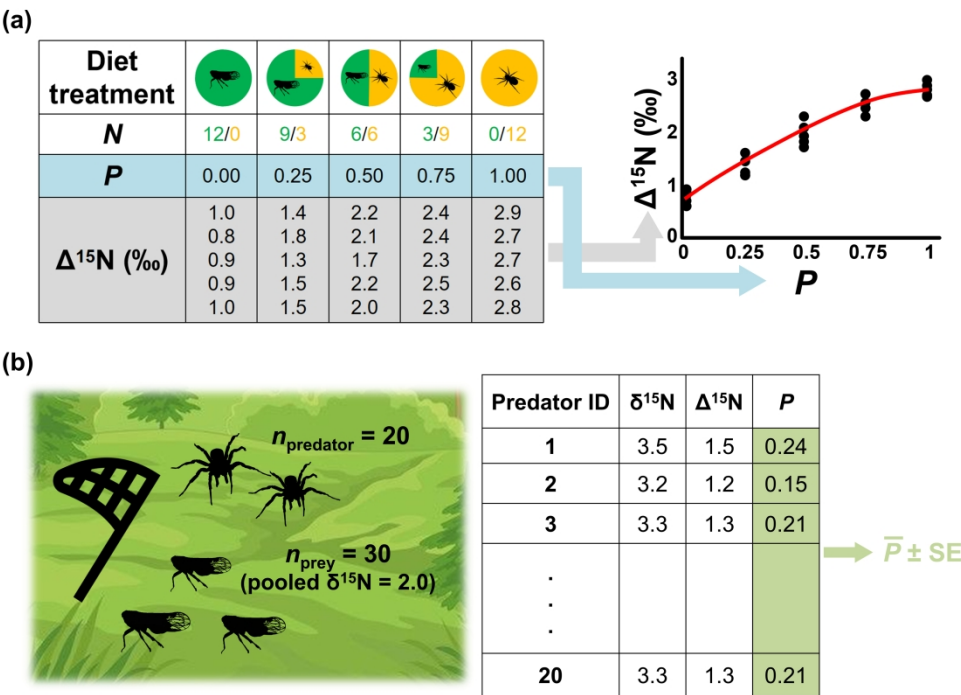| Predator ID	δ¹⁵N	Δ¹⁵N	P
1	3.5	1.5	0.24
2	3.2	1.2	0.15
3	3.3	1.3	0.21
.			
.			
.			
20	3.3	1.3	0.21

$\overline{P} \pm SE$

Figure 2. A hypothetical example of (a) standard IGP curve construction using data collected from the second feeding trial and (b) estimation of IGP with field samples of top predator and shared prey. N: number of shared prey/mesopredator in the mixed diet; P: proportion of mesopredator consumed (%).

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