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What's for dinner? Diet and trophic impact of an invasive anuran *Hoplobatrachus tigerinus* on the Andaman archipelago

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Amphibian invasions have considerable detrimental impacts on recipient ecosystems; however, reliable risk analysis of invasive amphibians still requires research on more non-native amphibian species. An invasive population of the Indian bullfrog, *Hoplobatrachus tigerinus*, is currently spreading on the Andaman archipelago and may have significant trophic impacts on native anurans through competition and predation. We assessed the diet of the invasive *Hoplobatrachus tigerinus* (n = 358), the native *Limnonectes* spp. (n = 375) and *Fejervarya* spp. (n = 65) in three sites, across four habitat types and two seasons, on the Andaman archipelago. We found a significant dietary overlap of *H. tigerinus* with *Limnonectes* spp., which may lead to competition. Small vertebrates, including several endemic species, constituted a majority of *H. tigerinus* diet by volume, suggesting potential impact by predation. Diets of the three species were mostly governed by the positive relationship between predator-prey body sizes. Niche breadth analyses did not indicate any significant changes in diet between seasons. *Hoplobatrachus tigerinus* and *Fejervarya* spp. chose evasive prey, suggesting that these two species are mostly ambush predators; *Limnonectes* spp. elected sedentary prey; although a large portion of its diet consisted of other prey types, such electivity indicates 'active search' as its major foraging strategy. All three species of anurans mostly consumed terrestrial prey. This intensive study on a new genus of invasive amphibian contributes to the knowledge on impacts of amphibian invasions, and elucidates the feeding ecology of *H. tigerinus*, and species of the genera *Limnonectes* and *Fejervarya*. We stress on the necessity to evaluate prey availability and volume in future studies for meaningful insights into diet of amphibians.

1 **What's for dinner? – Diet and trophic impact of an invasive anuran *Hoplobatrachus tigerinus***
2 **on the Andaman archipelago**

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11 **ABSTRACT**

12 Amphibian invasions have considerable detrimental impacts on recipient ecosystems. However,
13 reliable risk analysis of invasive amphibians still requires research on more non-native
14 amphibian species. An invasive population of the Indian bullfrog, *Hoplobatrachus tigerinus*, is
15 currently spreading on the Andaman archipelago and may have significant trophic impacts on
16 native anurans through competition and predation. We assessed the diet of the invasive
17 *Hoplobatrachus tigerinus* (n = 358), and native *Limnonectes* spp. (n = 375) and *Fejervarya* spp.
18 (n = 65) in three sites, across four habitat types and two seasons, on the Andaman archipelago.
19 We found a significant dietary overlap of *H. tigerinus* with *Limnonectes* spp. Small vertebrates,
20 including several endemic species, constituted the majority of *H. tigerinus* diet by volume,

21 suggesting potential impact by predation. Diets of the three species were mostly governed by
22 the positive relationship between predator-prey body sizes. Niche breadth analyses did not
23 indicate any significant changes in diet between seasons. *Hoplobatrachus tigerinus* and
24 *Fejervarya* spp. chose evasive prey, suggesting that these two species are mostly ambush
25 predators; *Limnonectes* spp. elected sedentary prey; although a large portion of its diet
26 consisted of evasive prey, such electivity indicates 'active search' as its major foraging strategy.
27 All three species of anurans mostly consumed terrestrial prey. This intensive study on a genus
28 of newly invasive amphibian contributes to the knowledge on impacts of amphibian invasions,
29 and elucidates the feeding ecology of *H. tigerinus*, and species of the genera *Limnonectes* and
30 *Fejervarya*. We stress the necessity to evaluate prey availability and volume in future studies for
31 meaningful insights into diet of amphibians.

32 Key Words: diet overlap, ecological niche, resource use, predator-prey, food electivity;
33 Dicoglossidae; invasive impact; Anura

34 INTRODUCTION

35 Accelerating rates of biological invasions (Seebens et al., 2017) and their consequent negative
36 impacts (Simberloff et al., 2013) have led to increased efforts towards pre-invasion risk
37 assessment and prioritization based on impacts (van Wilgen et al. *in review*; Blackburn et al.,
38 2014). Amphibian invasions have considerable detrimental impacts on recipient ecosystems
39 (Pitt et al., 2005; Kraus, 2015), the magnitude of impact being comparable to that of invasive
40 freshwater fish and birds (Measey et al., 2016). Impact mechanisms of amphibian invaders
41 remain relatively understudied (Crossland et al., 2008) and are varied. Impact via predation and

42 competition (*sensu* Blackburn et al., 2014) in particular has been frequently examined, with
43 documented impact on invertebrates (Greenlees et al. 2006; Choi and Beard 2012; Shine 2010),
44 fishes (Lafferty and Page 1997), amphibians (Kats & Ferrer, 2003; Wu et al., 2005; Measey et al.,
45 2015; but see Greenlees et al., 2007) and birds (Boland, 2004), though other taxa may also be
46 affected (Beard & Pitt, 2005).

47 However, reliable risk analysis of invasive amphibians still requires research on more non-native
48 amphibian species (van Wilgen et al., *in review*), as the existing knowledge on impacts is mostly
49 based on the cane toad *Rhinella marina* and the American bullfrog *Lithobates catesbianus*
50 (Measey et al., 2016; van Wilgen et al., *in review*). Comparisons of impact across taxonomic
51 groups for management prioritization (Blackburn et al., 2014; Kumschick et al., 2015) may also
52 be impeded by the relatively understudied category of amphibian invasions as compared to
53 other vertebrate invasions (Pyšek et al., 2008). This knowledge gap is further compounded by
54 geographic biases in invasion research, with limited coverage in Asia and Africa (Pyšek et al.,
55 2008); developing countries also have relatively less invasion research (Nunez & Pauchard 2010;
56 Measey et al., 2016).

57 An invasive population of the Indian bullfrog, *Hoplobatrachus tigerinus* (Daudin, 1802), is
58 currently spreading on the Andaman archipelago, Bay of Bengal, following its introduction in
59 the early 2000s (Mohanty & Measey, *in review*). The bullfrog has its native range on the Indian
60 sub-continent encompassing low to moderate elevations in Nepal, Bhutan, Myanmar,
61 Bangladesh, India, Pakistan, and Afghanistan (Dutta, 1997). The bullfrog has previously been
62 introduced to Madagascar (Glaw & Vences, 2007), and possibly to the Maldives (Dutta, 1997)

63 and Laccadive Islands (Gardiner 1906). This large bodied frog (up to 160 mm) has high
64 reproductive potential (up to 20,000 eggs per clutch, Khan & Malik 1987) and is uncommon or
65 absent in forested and coastal regions, but occurs as a human commensal (Daniels 2005). It is
66 considered a dietary generalist, feeding on invertebrates and even large vertebrates such as
67 *Duttaphrynus melanostictus* (Padhye et al., 2008; Datta & Khaledin, 2017); however,
68 quantitative diet assessment with adequate sample size across habitats and seasons is lacking
69 (but see Khatiwada et al., 2016 for diet of *H. tigerinus* in rice fields of Nepal).

70 *Hoplobatrachus tigerinus* on the Andaman archipelago co-occurs with native anurans of the
71 genera *Duttaphrynus*, *Fejervarya*, *Limnonectes*, and *Microhyla* (NPM unpublished data;
72 Harikrishnan et al., 2010). Given the large size of *H. tigerinus*, it is likely to feed on
73 proportionately large prey, including amphibians and other vertebrates (Datta & Khaledin,
74 2017; Measey et al., 2015). The high volume of prey consumed by *H. tigerinus* (Padhye et al.,
75 2008) may lead to direct competition with native anurans, especially under relatively high
76 densities of *H. tigerinus* in human modified areas (Daniels, 2005). Although the diet of native
77 anurans has not been assessed on the Andaman Islands, *Fejervarya limnocharis* is considered to
78 be a generalist forager on terrestrial invertebrates (Hirai & Matsui, 2001), *Limnonectes* spp. are
79 known to feed on vertebrates in addition to arthropods (Emerson, Greene & Charnov 1994; Das
80 1996), and Microhylids and Bufonids are considered to be myrmecophagous. In terms of size, *H.*
81 *tigerinus* is much larger than native anurans of the Andaman archipelago (Fig. 1) and may
82 impact the native anurans through both predation and competition.

83 Niche overlap, in combination with prey availability (electivity), can be used to assess trophic
84 competition between species (e.g. Vogt et al., 2017). In addition to taxonomic evaluation and
85 enumeration of the prey consumed, it is crucial to consider prey volume and frequency of prey
86 occurrence to ascertain overall importance of a particular category of prey (Hirschfield & Rödel,
87 2011; Boelter et al., 2012; Choi and Beard 2012); classification by functional type (hardness and
88 motility of prey) is useful in understanding predator behaviour (Toft 1980; Vanhooydonck et al.,
89 2007; Carne & Measey 2013). Further, seasonality in prey availability may influence diet in
90 amphibians (Hodgkison & Hero 2003; de Oliveira & Haddad, 2015), therefore, there is also a
91 need to assess diet across seasons, to fully capture the range of prey. Another important driver
92 of prey choice may be the positive relationship between predator-prey body sizes (Werner et
93 al., 1995; Wu et al., 2005).

94 We aimed to assess the trophic impact of the invasive *Hoplobatrachus tigerinus* on the native
95 anurans of the Andaman Islands through competition and predation. We carried out diet
96 analyses of the invasive *H. tigerinus* and native anurans, across four habitat types and two
97 seasons, to ascertain the nature and magnitude of trophic impact. We hypothesized that i)
98 small vertebrates constitute a majority of the *H. tigerinus* diet, particularly, by volume and ii)
99 the diet of *H. tigerinus* significantly overlaps with the diet of native anurans, thereby, leading to
100 potential competition. Additionally, we aimed to characterize the predation behaviour of these
101 anurans in terms of electivity and predation strategy (ambush or active search).

102 **METHODS**

103 We carried out the study in the Andaman archipelago for six months, from February to July
104 2017. The Andaman archipelago is part of the Indo-Burma biodiversity hotspot (Myers et al.
105 2000) and with 40% endemism in herpetofauna (Harikrishnan et al., 2010). This group of nearly
106 300 islands is situated between 10°30'N to 13°40'N and 92°10'E to 93°10'E (Fig. 2). The tropical
107 archipelago receives an annual rainfall of 3000 mm to 3500 mm (Andrews and Sankaran 2002);
108 primary and secondary forests encompass nearly 87% of the entire archipelago (Forest
109 Statistics 2013), whereas the remaining human modified areas comprise of settlements,
110 agricultural fields, and plantations. Of the nine species of native amphibians recorded, four
111 species (*Ingerana charelsdarwinii*, *Blythophryne beryet*, *Microhyla chakrapani*, and *Fejervarya*
112 *andamanensis*) are endemic to the Andaman Islands (Das 1999; Harikrishnan et al., 2010;
113 Chandramouli et al., 2016), however, taxonomic uncertainties still persist (Chandramouli et al,
114 2015; Harikrishnan Surendran, *Pers. Comm.*). The range restricted *Ingerana charlesdarwinii*, the
115 semi-arboreal *Blythophryne beryet*, the arboreal *Kaloula baleata ghosi* and the littoral
116 *Fejervarya cancrivora* are unlikely to co-occur with *H. tigrinus* at present (Das 1999;
117 Chandramouli 2016; Chandramouli et al., 2016). Thus, we constrained our choice for
118 comparative species to those which were strictly syntopic. As the taxonomy of the Andaman
119 amphibians remains in flux, we limited our identifications to the genus level as the taxonomic
120 identities of these species are pending formal re-assessments (Chandramouli et al., 2015).
121 Hereafter, *Fejervarya* spp and *Limnonectes* spp are referred to as *Fejervarya* and *Limnonectes*,
122 respectively.

123 We conducted the study in two sites (Webi and Karmatang) on Middle Andaman Island and one
124 site (Wandoor) on South Andaman Island (Fig. 2). We chose sites with moderately old invasions

125 of *Hoplobatrachus tigerinus* (more than 3 years since establishment; Mohanty & Measey in
126 review), assuming that a relatively longer time since establishment would indicate an adequate
127 population to sample from. In each site, we established four 1 ha plots with varying land use-
128 land cover types: agriculture, plantations (Areca nut and Banana), disturbed (logged) and
129 undisturbed forest (minimal use). To capture the variation in diet with respect to seasons, we
130 carried out the sampling in both dry (January to April) and wet (May to July) seasons, the latter
131 coinciding with the south-westerly monsoon.

132 Our protocol was approved by the Research Ethics Committee: Animal Care and Use,
133 Stellenbosch University (#1260) and permission to capture anurans, was granted under the
134 permit of the Department of Environment and Forests, Andaman and Nicobar Islands
135 (#CWLW/WL/134/350). Diet of anurans was determined using stomach flushing, a standard and
136 low-risk technique to determine prey consumed (Patto, 1998; Solé et al., 2005). Anurans were
137 hand-captured between 1800 to 2200 hrs; stomach flushing was carried out within 3 h of
138 capture. We consciously avoided capture bias towards any particular size class, by actively
139 searching for anurans of all size classes. As our sampling focussed on sub-adult and adult
140 *Hoplobatrachus tigerinus* and was completed in July (presumably before breeding and
141 emergence of metamorphs) we did not examine the diet of metamorphs. In order to avoid
142 mortality, we did not stomach flush individuals below 20 mm SVL and hence, individuals of co-
143 occurring *Microhyla chakrapanii* (ca. 10-30 mm SVL; Pillai, 1977) were not sampled. After
144 excluding native anurans which did not co-occur with *H. tigerinus*, we sampled *Duttaphrynus*
145 *melanostictus* (although its taxonomic and geographic status is uncertain, Das 1999),
146 *Limnonectes spp.*, and *Fejervarya spp.* (hereafter, *Limnonectes* and *Fejervarya*). We conducted

147 stomach flushing using a syringe (3 ml to 10 ml for anurans of 20 mm-50 mm SVL and 60 ml for
148 anurans >60 mm SVL), soft infusion tube, and water from site of capture. In addition to SVL, we
149 noted the sex and measured head width (HW) and lower jaw length length (LJL) of the anurans.
150 The stomach flushed individuals were toe-clipped (following Hero, 1989; Grafe et al., 2011) to
151 ensure that sampling bias, if any, was recorded. Individuals were released back to the capture
152 site post completion of the procedure.

153 We collected the expelled prey items in a transparent beaker and sieved the contents using a
154 mesh of 0.5 mm. Prey items from each individual were classified up to a minimum of order
155 level, and further characterized by functional traits (hardness and motility, following
156 Vanhooydock et al., 2007). Length and width of intact prey were measured under an 8x
157 magnifying lens to the nearest 0.01 mm using a Vernier calliper and recorded along with the
158 prey's life stage (adult/larvae). We preserved all prey items in 70% ethanol.

159 We also determined electivity of prey, based on prey consumption as compared to prey
160 availability. Terrestrial prey were measured using five pitfall traps in each 1 ha plot, which were
161 visited twice daily for a duration of three days (total of 30 trap occasions). Within each 1 ha
162 plot, the pitfalls were arranged in the four corners and one in the centre of the plot. We used
163 plastic traps, 80 mm in diameter and 300 mm high. A wet cloth was kept at the bottom to
164 provide refuge to trapped animals, so as to prevent any predation before sample collection. We
165 used chloroform soaked cotton balls to euthanize the invertebrate prey, prior to collection.
166 These prey items were also identified up to the order level and measured for length and width.

167 Our approach of estimating prey availability excludes flying evasive orders (e.g. adult
168 lepidopterans) and vertebrate prey.

169 *Data analyses*

170 We did not obtain adequate numbers of *Duttaphrynus melanostictus* (n = 4) individuals and
171 hence they were not included in the analyses. We pooled samples from the three sites to
172 examine the diet of the three species of anurans. At the species level, we assessed the number,
173 volume, and frequency (number of individuals with a given prey item in their stomach) of
174 consumed prey under each taxonomic category. Volume was calculated using the formula of an
175 ellipsoid, following Colli and Zamboni (1999),

$$176 \text{ volume} = \frac{4}{3}\pi \left(\frac{l}{3}\right) \left(\frac{w}{3}\right)^2 ,$$

177 where, l is prey length and w is prey width. Prey items for which volume could not be calculated
178 due to lack of measurement data (i.e. fragmented prey) were assigned the median prey volume
179 for that order.

180 In order to assess the overall importance of a prey category, based on the percentage of
181 number, frequency and volume, we used the Index of Relative Importance (IRI, Pinkas et al.,
182 1971). We characterized the niche breadth of each anuran species with the Shannon-Weaver's
183 measure of evenness (J'), which is a modified from the Shannon-Weaver index (H' , Shannon
184 and Weaver 1964). For the niche breadth analyses, we only included habitat types where the
185 *Hoplobatrachus tigerinus* and the native anurans co-occurred (plantation and agriculture); we

186 did not find *H. tigrinus* in undisturbed and disturbed forest plots, although there have been
187 observations of a few individuals along forest streams (Harikrishnan & Vasudevan, 2013).
188 To test for diet overlap between the three species, we employed the MacArthur and Levins'
189 index *Ojk* (MacArthur and Levins 1967) in the *pgirmess* package (Giraudoux 2017); we built null
190 models using the 'niche_null_model' function of the *EcoSimR* package (Gotelli et al. 2015) to
191 test for statistical significance of *Ojk*. We also assessed prey availability for each site across both
192 dry and wet seasons, using the Simpson's diversity index (Supplemental Information 1). We
193 determined electivity of terrestrial invertebrate prey by the three species of anurans, using the
194 Relativized Electivity Index (Vanderploeg & Scavia 1979). Following Measey (1998), we
195 computed electivity for only those prey taxa with $n \geq 10$ prey items for *Hoplobatrachus tigrinus*
196 and *Limnonectes*; given the low sample size for *Fejervarya* (Table 1), we fixed the cut-off at $n \geq$
197 5. Further, electivity for *H. tigrinus* was calculated only for agriculture and plantations;
198 electivity for *Fejervarya* was considered only for one site with adequate sample size: Wandoor
199 (Table 1). All analyses were carried out in the statistical software R 3.4.1 (R Core Team 2017).

200 RESULTS

201 Overall, we sampled 798 individuals of two native anurans and the invasive *Hoplobatrachus*
202 *tigrinus* (Table 1). We obtained 1478 prey items belonging to 35 taxonomic categories in the
203 stomach of 688 anurans (Table 2, Supplemental Information 2). Vacuity index (i.e. proportion of
204 empty stomachs) was higher in the dry season (19.68%) as compared to the wet season
205 (8.67%). Less than 4% of prey items remained unidentified, mostly due to advanced levels of
206 digestion. *Hoplobatrachus tigrinus* consumed prey items under the most numbers of

207 taxonomic categories (29), followed by *Limnonectes* (25), and *Fejervarya* (14). Vertebrates were
208 consumed by both *H. tigerinus* and *Limnonectes*, although the numeric and volumetric
209 percentage of vertebrates consumed was higher in the case of *H. tigerinus* (2.62%, 58.03%) as
210 compared to *Limnonectes* (0.48%, 5.16%; Table 2). Based on IRI, coleopterans and orthopterans
211 constituted the major prey of *H. tigerinus* and *Limnonectes*, whereas, formicids and
212 coleopterans formed the majority in the diet of *Fejervarya* (Table 2).

213 Niche breadth (J') varied only slightly between dry and wet seasons in all three anurans (Fig. 3).
214 It was highest for *Limnonectes*, followed by *Hoplobatrachus tigerinus*, and *Fejervarya* (Fig. 3).
215 The diet of *H. tigerinus* overlapped significantly with that of *Limnonectes* ($Ojk = 0.87$, lower-tail
216 $p > 0.999$, upper-tail $p < 0.001$) but there was no significant overlap with *Fejervarya* ($Ojk = 0.35$,
217 lower-tail $p = 0.919$, upper-tail $p = 0.08$). The diet of the two native anurans overlapped
218 significantly ($Ojk = 0.58$, lower-tail $p = 0.967$, upper-tail $p = 0.03$).

219 Based on availability of terrestrial invertebrates, prey electivity of all three species appeared to
220 be driven by the relationship between predator-prey body sizes (Fig. 4). While the largest
221 species, *Hoplobatrachus tigerinus*, strongly selected for moderately large to large prey (≥ 100
222 mm^3), the smallest anuran, *Fejervarya*, selected for prey items smaller than $<10 \text{ mm}^3$; the
223 medium sized *Limnonectes* chose small and moderately large prey items ($10 \text{ mm}^3 - 500 \text{ mm}^3$),
224 although the magnitude of electivity (positive or negative) was lowest for this species (Fig. 1;
225 Fig. 4). Most of the prey consumed by the three species was terrestrial, hard, and evasive; diet
226 of *Limnonectes* included a relatively high proportion of soft and sedentary prey.

227 We observed several endemic vertebrate species in the diet of *H. tigerinus*, including the
228 Andaman emerald gecko *Phelsuma andamanensis*, Chakrapani's narrow mouthed frog
229 *Microhyla chakrapani*, the Andaman skink *Eutropis andamanensis*, and Oates's blind snake
230 *Typhlops oatesii*. We also found *Limnonectes*, one unidentified rodent, and the invasive
231 *Calotes versicolor* in the diet of *H. tigerinus*.

232 DISCUSSION

233 We expected the diet of *H. tigerinus* to overlap significantly with the diet of both species of
234 native anurans. However, we found a significant overlap only with *Limnonectes*, such that when
235 prey is limited competition may arise. As expected, small vertebrates constituted a majority of
236 *H. tigerinus* diet by volume, suggesting potential impact by predation on a large proportion of
237 the endemic island fauna. Diets of the three species were mostly governed by a strong positive
238 relationship between predator-prey body sizes. Niche breadth analyses did not indicate
239 significant changes in diet between seasons.

240 We observed 86% niche overlap between *Hoplobatrachus tigerinus* and *Limnonectes*, which
241 was statistically significant in comparison to the constructed null model; whereas, niche overlap
242 of *H. tigerinus* with *Fejervarya* was not significant. On the other hand, prey electivity (based on
243 prey availability) suggests that *H. tigerinus* strongly elected for moderately large to large prey
244 whereas small and moderately large prey were elected by *Limnonectes* (Fig. 4). This may result
245 in competition for prey ranging from 10 – 500 mm³ between the two species, under the
246 conditions of limited prey. Although there was a clear positive relationship between predator-
247 prey body sizes at the species level (Fig. 4), we did not observe increased dietary overlap (in

248 terms of prey taxa) for relatively large *Limnonectes* and relatively small *H. tigerinus*. Trophic
249 competition in amphibians may lead to a decrease in fitness (e.g. growth rate) and affect
250 population level processes (Benard & Maher, 2011). Impact of invasive amphibians (post-
251 metamorphic) via trophic competition has been documented in fewer studies as compared to
252 predation (Measey et al., 2016), but this mechanism may affect taxa at various trophic levels
253 (Smith et al., 2016). Metamorphs of *H. tigerinus* may also compete with both *Fejervarya* and
254 *Limnonectes* as they would fall under the same size class (20 mm-60mm; Daniels, 2005).
255 Although our sampling did not evaluate the diet of *H. tigerinus* metamorphs, we think this may
256 be relevant as competition between juvenile *Lithobates catesbianus* and small native anurans
257 has been previously documented in Daishan Island, China (Wu et al., 2005).

258 Evaluating dietary overlap is a pre-cursor to determining trophic competition due to invasive
259 populations, which do not have shared evolutionary history with native species. Dietary overlap
260 in co-occurring species may be independently influenced by prey availability (Kuzmin, 1995),
261 prey taxa (Lima, 1998), prey size (Toft, 1981; Vignoli et al., 2009; Crnobrnja-Isailović, 2012) and
262 a combination of these factors. Therefore, it is essential to design studies and interpret diet
263 patterns with reference to all three factors, in order to arrive at meaningful inferences on prey
264 consumed, dietary overlap, and probable subsequent competition (Kuzmin, 1990; but see
265 Kuzmin, 1995 regarding criteria for competition). Further, prey size should ideally be measured
266 in terms of volume, as it is known to be a better dietary descriptor (Vignoli & Luiselli 2012).

267 *Hoplobatrachus tigerinus* preyed upon three classes of vertebrates (Amphibia, Reptilia, and
268 Mammalia), which accounted for a significant proportion of its diet by volume, although

269 vertebrate prey was numerically inferior to invertebrates in the diet. Such major contribution to
270 the volume of prey by vertebrates (despite numerical inferiority) has been observed for
271 *Lithobates catesbianus* and *Xenopus laevis* (Boelter et al., 2012; Vogt et al., 2017); anurophagy
272 may also contribute significantly to the diet of many amphibians (Measey et al., 2015; Courant
273 et al., 2017). We observed several endemic species in the diet of *H. tigrinus*, which may be
274 vulnerable if frequently preyed upon. *Limnonectes* was also consumed by *H. tigrinus*, thereby,
275 indicating a potential two-pronged impact through predation and competition. However,
276 demographic change (if any) in *Limnonectes*, due to predation and competition by *H. tigrinus*,
277 was not evaluated in this study. The invasive *H. tigrinus* on the Andaman Islands reportedly
278 consume poultry (Manish Chandi pers comm., Mohanty & Measey, *in review*) and stream fish
279 (NPM unpublished data). Despite the presence of a large portion of vertebrates in the diet of *H.*
280 *tigrinus*, its trophic position (consistency of vertebrate prey consumption) can only be
281 ascertained with stable isotope analyses (Huckembeck et al., 2014). Although, diet analysis of
282 invasive species can identify vulnerable taxa and confirm at least ‘minimal’ to ‘minor’ levels of
283 impact through predation and competition (*sensu* Blackburn et al., 2014; Hawkins et al. 2015),
284 such analysis must be complimented with evidence of trophic level effects to evaluate the
285 degree of impact (Smith et al., 2016).

286 The large proportion of ants in the diet of *Fejervarya* does not necessarily prove specialization
287 for myrmecophagy. Hirai and Matsui (2000) inferred relatively weaker avoidance of ants by
288 *Glandirana rugosa* as compared to other anurans. Although we found the same pattern for
289 *Fejervarya* based on prey electivity ($E = -0.02$), it does not prove weak avoidance either. As
290 social insects, ants may be disproportionately captured in the pitfall traps, it is necessary to

291 compliment diet studies on potentially myrmecophagous predators with additional evidence (e. g.
292 cafeteria experiments). *Hoplobatrachus tigerinus* and *Fejervarya* chose evasive prey, suggesting
293 that these two species are mostly ambush ('sit and wait') predators; *Limnonectes* elected
294 sedentary prey along with other prey types, indicating a combination of 'active search' and 'sit
295 and wait' foraging (Huey & Pianka, 1981; Vanhooydonck et al., 2007). Generally, soft bodied
296 prey are considered to provide more nutrition by size as compared to hard prey and therefore,
297 it is hypothesized that species will select soft prey more often than hard prey, which in turn is
298 dependent on prey availability by season (Measey et al., 2011; Carne & Measey 2013).
299 However, we find that diet does not vary considerably across the seasons (Fig. 3) and is
300 governed more by size than hardness of prey (Fig. 4; Werner et al., 1995).

301 Although our sampling for diet analysis by stomach flushing was adequate (Table 1), our
302 assessment of prey availability did not include flying invertebrates and vertebrates, which
303 prevents us from carrying out electivity analyses on these taxa.

304 **CONCLUSION**

305 Diet analyses of *Hoplobatrachus tigerinus* revealed significant predation on endemic
306 vertebrates and a high diet overlap with large-bodied native anurans, indicating direct
307 predation. Given the observed high density of *H. tigerinus* in human modified habitats on the
308 Andaman archipelago (NPM unpublished data), trophic competition and predation by *H.*
309 *tigerinus* may have a significant impact on native anuran populations in these habitats. In
310 addition to quantifying the trophic niche of anurans belonging to three genera, we stress the

311 necessity to evaluate prey availability and volume in future studies for meaningful insights into
312 diet of amphibians.

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Figure 1(on next page)

Snout-vent length of three species of anurans used for diet assessment.

Individuals belong to the invasive Indian bullfrog *Hoplobatrachus tigerinus* and the native *Limnonectes* spp. and *Fejervarya* spp., sampled at three locations on the Andaman archipelago.

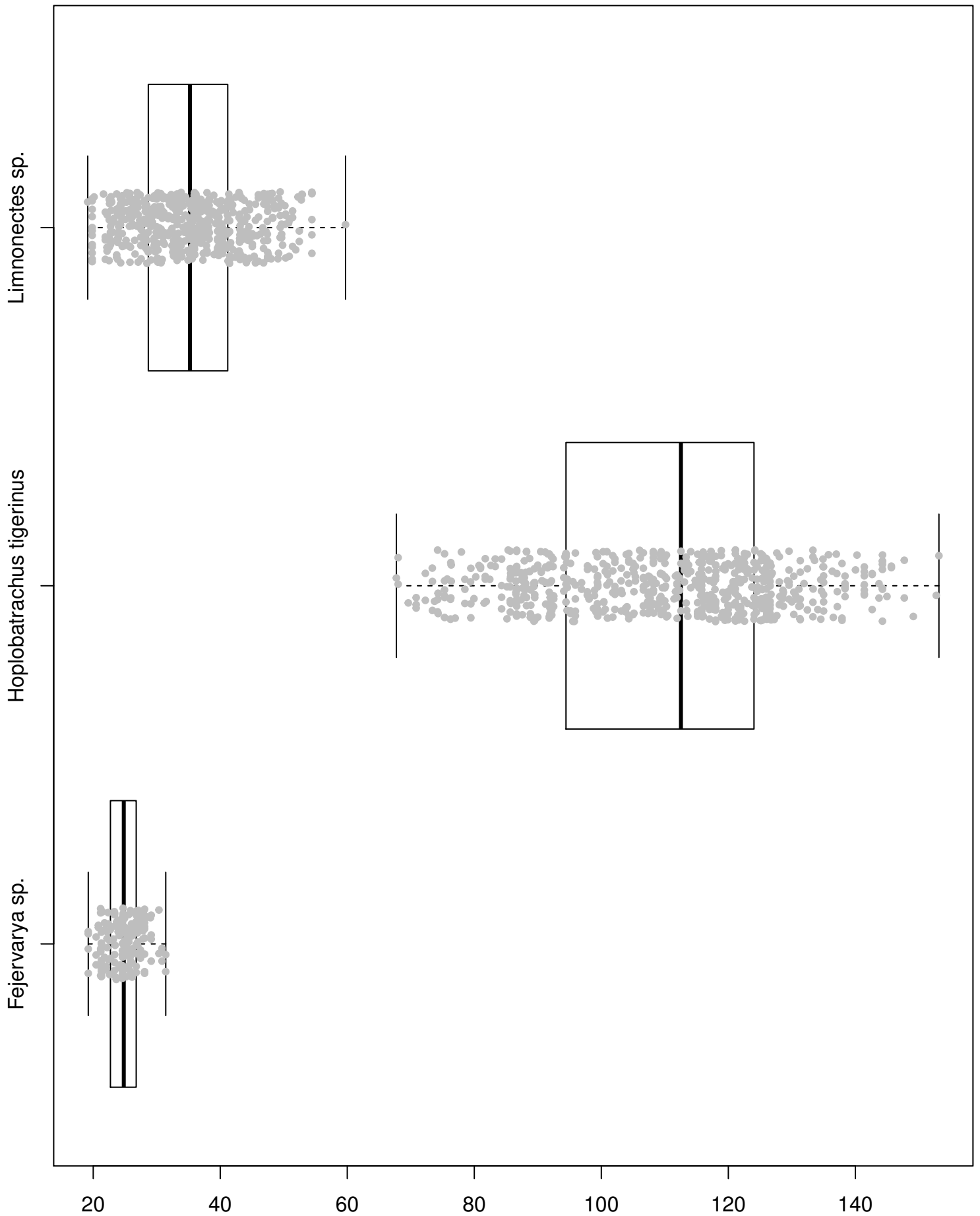


Figure 2

Study area map showing the major islands of the Andaman archipelago and the three sampling locations.

Diet assessment of *Hoplobatrachus tigerinus*, *Limnonectes* spp., and *Fejervarya* spp. were carried out from February 2017 - July 2017.

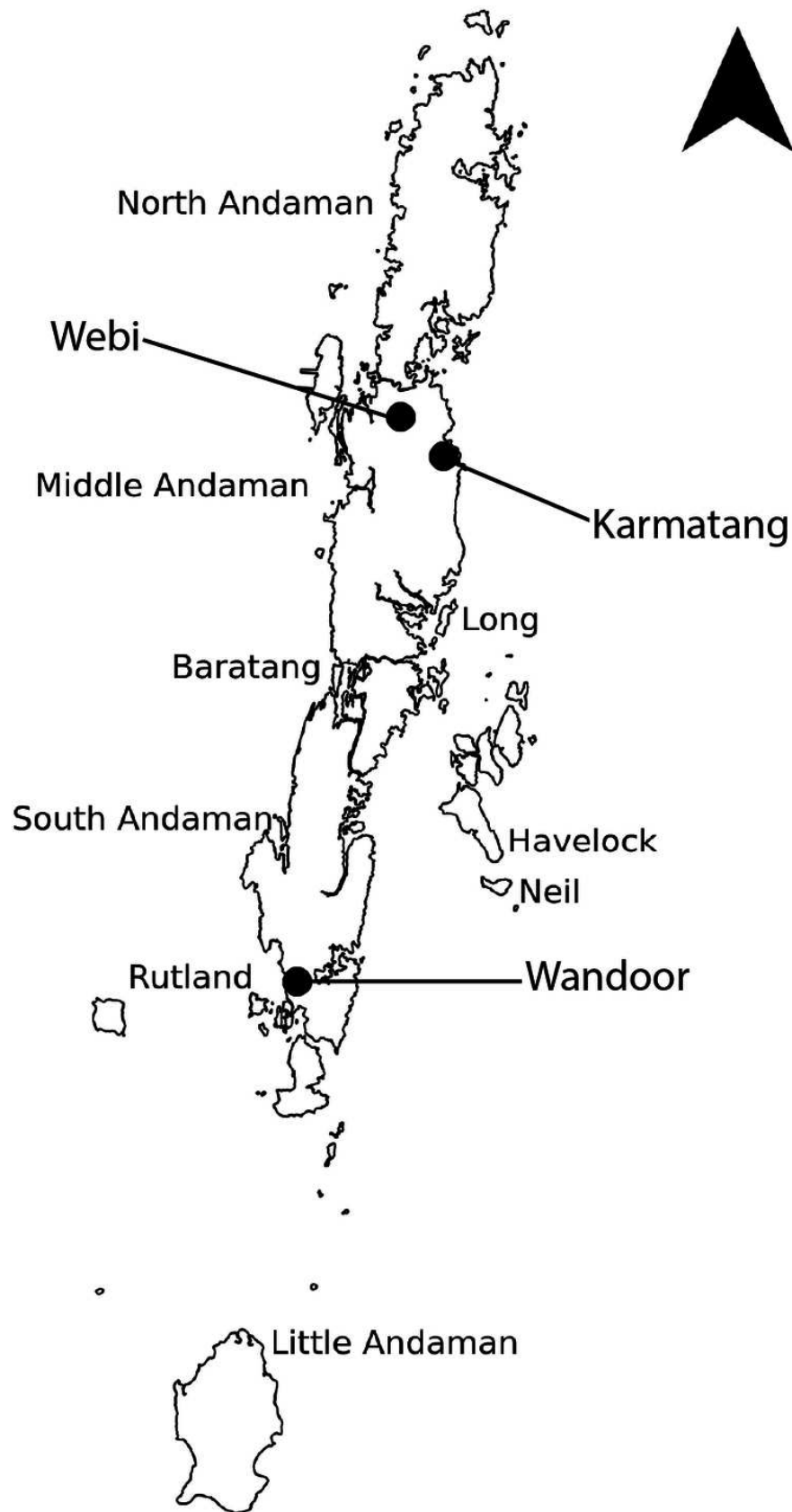


Figure 3

Niche breadth (J') of the invasive *Hoplobatrachustigerinus* and the native *Limnonectes* spp. and *Fejervarya* spp., across dry (February-April) and wet seasons (May-July).

Niche breadth calculated for anuran individuals captured from agricultural fields and plantations, where both invasive and native anurans co-occur at the three sampling locations on the Andaman archipelago.

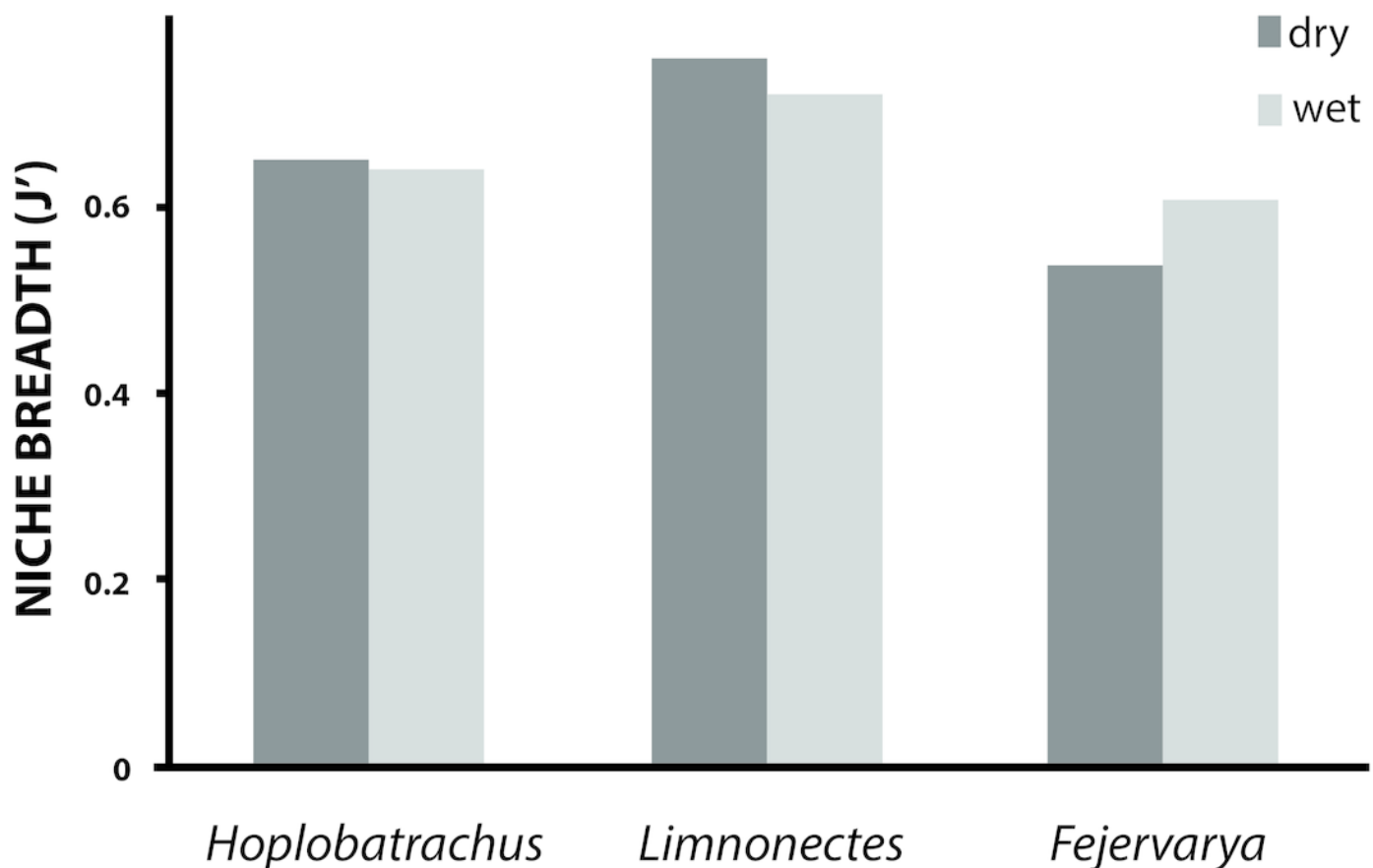


Figure 4

Prey electivity in terms of volume, by the invasive *Hoplobatrachustigerinus* and native *Limnonectes* spp. and *Fejervarya* spp.

Prey electivity based on prey consumption and availability, at three sites on the Andaman archipelago.

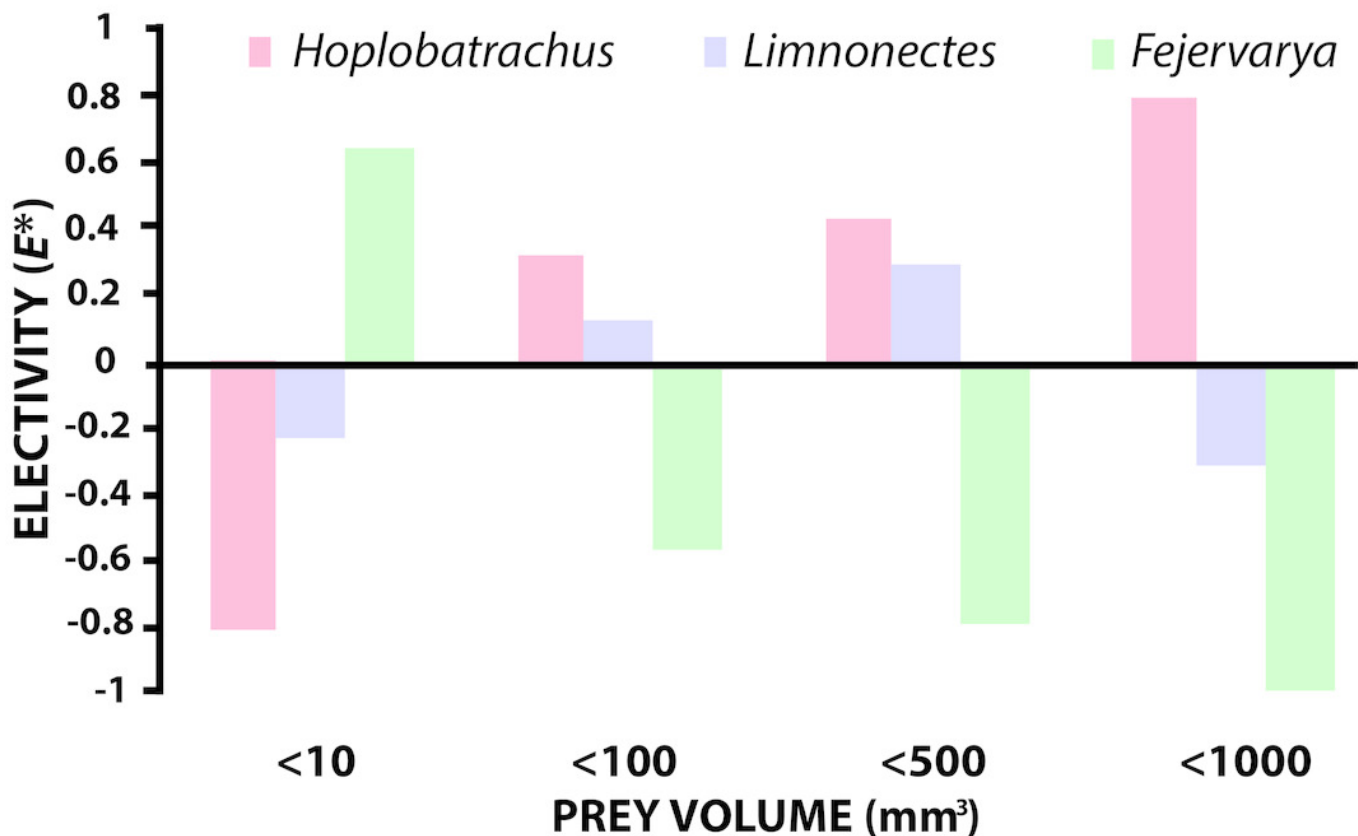


Table 1 (on next page)

Sampling effort for diet assessment of the invasive *Hoplobatrachus tigerinus* and native *Limnonectes* spp. and *Fejervarya* spp.

Sampling carried out in four habitat types across two seasons, at three sampling locations on the Andaman Islands.

1 **Table 1:** Sampling effort for diet assessment of the invasive *Hoplobatrachus tigerinus* and native
 2 *Limnonectes* spp. and *Fejervarya* spp. Sampling carried out in four habitat types across two
 3 seasons, at three sampling locations on the Andaman Islands.

4

	Agriculture		Plantation		Disturbed Forest		Undisturbed Forest	
	dry	wet	dry	wet	dry	wet	dry	wet
<i>H. tigerinus</i>								
Karmatang	41	35	29	29	0	0	0	0
Webi	32	35	48	38	0	0	0	0
Wandoor	0	0	38	33	0	0	0	0
<i>Limnonectes</i>								
Karmatang	0	17	5	26	0	25	0	22
Webi	14	17	19	26	13	17	13	17
Wandoor	7	21	17	29	19	11	30	10
<i>Fejervarya</i>								
Karmatang	0	0	0	0	0	0	0	0
Webi	1	0	0	0	1	0	0	0
Wandoor	19	17	13	2	10	0	2	0

5

6

Table 2 (on next page)

Diet of three species of anurans on the Andamanarchipelago

Diet of *Hoplobatrachus tigerinus*, *Limnonectes* spp. and *Fejervarya* spp. described in terms of percentage N - prey abundance, V - volume, F - frequency of occurrence in anurans, and IRI - Index of relative importance.

1 **Table 2:** Diet of three species of anurans on the Andaman archipelago, described in terms of percentage N – prey abundance, V –
 2 volume, F – frequency of occurrence in anurans, and IRI – Index of relative importance.

3

	<i>Hoplobatrachus tigerinus</i>				<i>Limnonectes</i>				<i>Fejervarya</i>			
Prey	N%	V%	F%	IRI	N%	V%	F%	IRI	N%	V%	F%	IRI
Acari	0	0	0	0	0.32	0.006	0.39	0.12	0.57	0.14	0.84	0.61
Agamidae	0.43	50.44	0.57	29.07	0	0	0	0	0	0	0	0
Amphipoda	0	0	0	0	0.48	0.07	0.58	0.32	0	0	0	0
Anura	0.87	4.95	1.14	6.65	0.32	5.12	0.39	2.12	0	0	0	0
Aranae	3.20	0.73	4	15.74	7.60	2.27	8.59	84.93	7.51	7.75	10.16	155.23
Arthropoda	6.55	0	8.57	56.22	5.50	0	6.64	36.53	0.57	0	0.84	0.48
Blattaria	1.45	0.33	1.90	3.42	1.29	0.71	1.56	3.14	0	0	0	0
Chilopoda	3.35	6.15	2.85	27.15	3.23	2.75	3.9	23.41	1.15	7.62	1.69	14.88
Coleoptera	29.73	12.14	24.57	1029.14	15.85	10.34	15.42	404.29	9.24	20.50	12.71	378.16
Crab	0.58	2.40	0.76	2.27	0.16	0.81	0.19	0.19	0	0	0	0

Dermaptera	0.14	0.009	0.19	0.02	1.61	0.20	1.95	3.55	0	0	0	0
Diplopoda	0.87	0.07	0.76	0.72	3.55	0.73	3.12	13.41	0	0	0	0
Diptera	1.89	0.56	1.52	3.74	4.04	0.09	3.9	16.15	14.45	3.38	14.40	256.95
Formicidae	3.93	0.37	3.80	16.42	10.19	0.24	8.00	83.58	38.72	5.80	23.72	1056.60
Gastropoda	4.22	0.71	4	19.76	3.23	1.5	3.32	15.72	0	0	0	0
Geckonnidae	0.14	0.45	0.19	0.11	0	0	0	0	0	0	0	0
Hemiptera	0.58	0.19	0.76	0.59	2.10	0.35	2.34	5.77	5.20	10.96	5.08	82.18
Hymenoptera	0.14	0.004	0.19	0.02	0	0	0	0	1.15	0.86	0.84	1.70
Insecta	1.45	0	1.90	2.77	1.29	0	1.36	1.76	6.35	0	9.32	59.27
Isoptera	2.62	0.24	2.09	6.01	7.44	1.88	4.49	41.89	2.31	0.87	3.38	10.81
Lacertidae	0.29	0.90	0.38	0.45	0	0	0	0	0	0	0	0
Lepidoptera	1.31	0.24	1.33	2.07	0.48	0.14	0.39	0.24	0	0	0	0
Leplarva	6.26	3.01	7.42	68.95	6.63	5.95	6.64	83.59	3.46	15.08	4.23	78.61
Mantodea	0.29	0.72	0.38	0.38	0	0	0	0	0	0	0	0
Odonata	0.72	0.07	0.95	0.76	0.16	0.04	0.19	0.04	0	0	0	0

Oligochaeta	1.31	0.77	1.52	3.18	4.69	54.54	4.10	242.95	0	0	0	0
Opilionida	0	0	0	0	0	0	0	0	0	0	0	0
Orthoptera	24.48	12.62	24.19	897.74	13.26	9.45	14.84	337.34	3.46	20.01	5.08	119.39
Rodent	0.14	0	0.19	0.02	0	0	0	0	0	0	0	0
Scincidae	0.14	0.62	0.19	0.14	0	0	0	0	0	0	0	0
Serpentes	0.58	0.67	0.76	0.95	0.16	0.04	0.19	0.04	0	0	0	0
Siphonaptera	0	0	0	0	0	0	0	0	0.57	0.075	0.84	0.55
Slug	0.29	0.27	0.38	0.21	0.80	1.97	0.78	2.17	0	0	0	0
Unidentified	1.89	0.26	2.47	5.35	5.33	0.69	6.44	38.87	5.20	6.92	6.77	82.19
Zygentoma	0	0	0	0	0.16	0.01	0.19	0.03	0	0	0	0