What’s for dinner? Diet and potential 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 carried out diet analyses of the invasive *H. tigerinus* and native anurans, across four habitat types and two seasons; we hypothesized that i) small vertebrates constitute a majority of the *H. tigerinus* diet, particularly, by volume and ii) the diet of *H. tigerinus* significantly overlaps with the diet of native anurans, thereby, leading to potential competition. We assessed the diet of the invasive *Hoplobatrachus tigerinus* (*n* = 358), and individuals of the genera *Limnonectes* (*n* = 375) and *Fejervarya* (*n* = 65) and found a significant dietary overlap of *H. tigerinus* with only *Limnonectes*. Small vertebrates, including several endemic species, constituted the majority of *H. tigerinus* diet by volume, suggesting potential impact by predation. Prey consumption and electivity of the three anurans indicated a positive relationship between predator-prey body sizes. Individuals of *Hoplobatrachus tigerinus* and *Fejervarya* chose evasive prey, suggesting that these two taxa are mostly ambush predators; individuals of *Limnonectes* elected sedentary prey; although a large portion of its diet consisted of evasive prey, such electivity indicates ‘active search’ as its major foraging strategy. All three species of anurans mostly consumed terrestrial prey. This intensive study on a genus of newly 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 also stress the necessity to evaluate prey availability and volume in future studies for meaningful insights into diet of amphibians.
What’s for dinner? – Diet and potential trophic impact of an invasive anuran *Hoplobatrachus tigerinus* on the Andaman archipelago

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ABSTRACT

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 carried out diet analyses of the invasive *H. tigerinus* and native anurans, across four habitat types and two seasons; we hypothesized that i) small vertebrates constitute a majority of the *H. tigerinus* diet, particularly, by volume and ii) the diet of *H. tigerinus* significantly overlaps with the diet of native anurans, thereby, leading to potential competition. We assessed the diet of the invasive *Hoplobatrachus tigerinus*...
(n = 358), and individuals of the genera *Limnonectes* (n = 375) and *Fejervarya* (n = 65) and found a significant dietary overlap of *H. tigerinus* with only *Limnonectes*. Small vertebrates, including several endemic species, constituted the 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. Individuals of *Hoplobatrachus tigerinus* and *Fejervarya* chose evasive prey, suggesting that these two taxa are mostly ambush predators; individuals of *Limnonectes* elected sedentary prey; although a large portion of its diet consisted of evasive prey, such electivity indicates ‘active search’ as its major foraging strategy. All three species of anurans mostly consumed terrestrial prey. This intensive study on a genus of newly 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 also stress the necessity to evaluate prey availability and volume in future studies for meaningful insights into diet of amphibians.

**INTRODUCTION**

Accelerating rates of biological invasions (Seebens et al., 2017) and their consequent negative impacts (Simberloff et al., 2013) have led to increased efforts towards pre-invasion risk assessment and prioritization based on impacts (Blackburn et al., 2014). Amphibian invasions have considerable detrimental impacts on recipient ecosystems (Pitt et al., 2005; Kraus, 2015), the magnitude of impact being comparable to that of invasive freshwater fish and birds (Measey et al., 2016). Impact mechanisms of amphibian invaders remain relatively understudied (Crossland et al., 2008) and are varied. Impact via predation and competition
(sensu Blackburn et al., 2014) has been documented on invertebrates (Greenlees et al., 2006; Choi and Beard 2012; Shine 2010), fishes (Lafferty and Page 1997), amphibians (Kats & Ferrer, 2003; Wu et al., 2005; Measey et al., 2015; Liu et al., 2015; but see Greenlees et al., 2007) and birds (Boland, 2004), though other taxa may also be affected (Beard & Pitt, 2005). Amphibian invaders may carry diseases (e.g. *Batrachochytrium dendrobatidis*; Garner et al., 2006; Liu et al., 2013) and cause reproductive interference (D’Amore et al., 2009), apart from several other ecological impacts (see Kraus, 2015 and Measey et al., 2016 for detailed assessments).

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

An invasive population of the Indian bullfrog, *Hoplobatrachus tigerinus* (Daudin, 1802), is currently spreading on the Andaman archipelago, Bay of Bengal (Mohanty & Measey, in review). The bullfrog was most likely introduced in early 2000s and its exponential expansion has occurred since 2009, resulting in invasive populations on six out of the eight human inhabited islands of the Andaman archipelago (Mohanty & Measey, in review). ‘Contaminants’
of fish culture trade and intentional ‘release’ are likely to be the primary pathways of introduction and post-introduction dispersal, facilitating introductions from the Indian mainland and inter-island transfers (Mohanty & Measey, in review). The bullfrog has its native range on the Indian sub-continent encompassing low to moderate elevations in Nepal, Bhutan, Myanmar, Bangladesh, India, Pakistan, and Afghanistan (Dutta, 1997). The bullfrog has previously been introduced to Madagascar (Glaw & Vences, 2007), and possibly to the Maldives (Dutta, 1997) and Laccadive Islands (Gardiner 1906). This large bodied frog (up to 160 mm) has high reproductive potential (up to 5750 eggs per clutch, Oliveira et al., 2017) and is uncommon or absent in forested and coastal regions but occurs as a human commensal in plantations and agricultural fields (Daniels 2005). It is considered a dietary generalist, feeding on invertebrates and even large anurans such as Duttaphrynus melanostictus (Padhye et al., 2008; Datta & Khaledin, 2017); however, quantitative diet assessment with adequate sample size across habitats and seasons is lacking (but see Khatiwada et al., 2016 for diet of H. tigerinus in rice fields of Nepal).

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

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

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

**METHODS**

We carried out the study in the Andaman archipelago for six months, from February to July 2017. The Andaman archipelago comprises nearly 300 islands (ca. 6400 km²) is situated between 10°30’N to 13°40’N and 92°10’E to 93°10’E (Fig. 2), which are part of the Indo-Burma biodiversity hotspot (Myers et al., 2000) with a 40% endemism level in herpetofauna (Harikrishnan et al., 2010). The tropical archipelago receives an annual rainfall of 3000 mm to 3500 mm (Andrews and Sankaran 2002); primary and secondary forests encompass nearly 87% of the entire archipelago (Forest Statistics 2013), whereas the remaining human modified areas comprise of settlements, agricultural fields, and plantations. Of the nine species of native amphibians recorded, five species (*Ingerana charelsdarwinii*, *Blythophryne beryet*, *Microhyla chakrapani*, *Kaloula ghoshi* and *Fejervarya andamanensis*) are endemic to the Andaman Islands (Das 1999; Harikrishnan et al., 2010; Chandramouli et al., 2016; Chandramouli et al., 2018), however, taxonomic uncertainties still persist (Chandramouli et al, 2015; Harikrishnan Surendran, Pers. Comm.). Post-metamorphic frogs of the range restricted *I. charlesdarwinii*, the semi-arboreal *B. beryet*, the arboreal *Kaloula ghosii* and the littoral *F. cancrivora* are unlikely to co-occur with *H. tigerinus* at present (Das 1999; Chandramouli 2016; Chandramouli et al., 2016). Thus, we constrained our choice for comparative species to those which were strictly
syntopic. As the taxonomy of the Andaman amphibians remains in flux, we limited our identifications to the genus level for species belonging to the genera *Fejervarya* and *Limnonectes*, which are pending formal re-assessments (Chandramouli et al., 2015). Currently, *L. doriae, L. hascheanus, Fejervarya limnocharis, F. andamanensis*, and *F. cancrivora* are considered members of these two genera in the Andaman Islands (Harikrishnan et al., 2010; Harikrishnan Surendran, Pers. Comm.). Hereafter, *Fejervarya* spp. and *Limnonectes* spp. are referred to as *Fejervarya* and *Limnonectes*, respectively.

We conducted the study at two sites (Webi and Karmatang) on Middle Andaman Island and at one site (Wandoor) on South Andaman Island (Fig. 2). We chose sites with moderately old invasions of *H. tigerinus* (more than 3 years since establishment; Mohanty & Measey in review), assuming that a relatively longer time since establishment would indicate an adequate population to sample from. In each site, we established four 1 ha plots with varying land use-land cover types: agriculture, plantations (Areca nut and Banana), disturbed (logged) and undisturbed forest (minimal use). To capture the variation in diet with respect to seasons, we carried out the sampling in both dry (January to April) and wet (May to July) seasons, the latter coinciding with the south-westerly monsoon.

Our protocol was approved by the Research Ethics Committee: Animal Care and Use, Stellenbosch University (#1260) and permission to capture anurans, was granted under the permit of the Department of Environment and Forests, Andaman and Nicobar Islands (#CWLW/WL/134/350). Diet of anurans was determined using stomach flushing, a standard and low-risk technique to determine prey consumed (Solé et al., 2005). Anurans were hand-
captured between 1800 to 2200 hrs; stomach flushing was carried out within 3 h of capture. We consciously avoided capture bias towards any particular size class, by actively searching for anurans of all size classes. As our sampling focussed on sub-adult and adult H. tigerinus and was completed in July (presumably before breeding and emergence of metamorphs) we did not examine the diet of metamorphs. In order to avoid mortality, we did not stomach flush individuals below 20 mm SVL and hence, individuals of co-occurring Microhyla chakrapanii (ca. 10-30 mm SVL; Pillai, 1977) were not sampled After excluding native anurans which did not co-occur with H. tigerinus, our samples included Duttaphrynus melanostictus (although its taxonomic and geographic status is uncertain, Das 1999), Limnonectes and Fejervarya. We conducted stomach flushing using a syringe (3 ml to 10 ml for anurans of 20 mm-50 mm SVL and 60 ml for anurans >60 mm SVL), soft infusion tube, and water from site of capture. In addition to SVL, we measured head width (HW) and lower jaw length (LJL) of the anurans, using a Vernier calliper (0.01 mm precision) and noted the sex. The stomach flushed individuals were toe-clipped (following Grafe et al., 2011) to record the total number of recaptures (n = 54). Individuals were released back to the capture site post completion of the procedure. We collected the expelled prey items in a transparent beaker and sieved the contents using a mesh of 0.5 mm. Prey items from each individual were classified up to a minimum of order level, and further characterized by functional traits (hardness and motility, following Vanhooydock et al., 2007). Length and width of intact prey were measured under an 8x magnifying lens to the nearest 0.01 mm using a Vernier calliper and recorded along with the prey’s life stage (adult/larvae). We preserved all prey items in 70% ethanol.
We also determined electivity of prey, based on prey consumption as compared to prey availability. Terrestrial prey were measured using five pitfall traps in each 1 ha plot, which were visited twice daily for a duration of three days (total of 30 trap occasions). Within each 1 ha plot, the pitfalls were arranged in the four corners and one in the centre of the plot. We used plastic traps, 80 mm in diameter and 300 mm high. A wet cloth was kept at the bottom to provide refuge to trapped animals, so as to prevent any predation before sample collection. We used chloroform soaked cotton balls to euthanize the invertebrate prey, prior to collection. These prey items were also identified up to the order level and measured for length and width. Our approach of estimating prey availability excludes flying evasive orders (e.g. adult lepidopterans) and vertebrate prey.

Data analyses

We did not obtain adequate numbers of *Duttaphrynus melanostictus* (n = 4) individuals and hence they were not included in the analyses. We pooled samples from the three sites to examine diet at the species level for *H. tigerinus* and genus level for *Limnonectes* and *Fejervarya*. We assessed the number, volume, and frequency (number of individuals with a given prey item in their stomach) of consumed prey under each taxonomic category. Volume was calculated using the formula of an ellipsoid, following Colli and Zamboni (1999),

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

where, l is prey length and w is prey width. Prey items for which volume could not be calculated due to lack of measurement data (i.e. fragmented prey) were assigned the median prey volume.
for that order. We carried out a generalized linear model to test the relationship between body
size of anurans (SVL) and prey volume, after accounting for taxonomic identity of anurans. We
log transformed SVL to adhere to the assumption of normality and cube root transformed prey
volume, prior to the analysis.

In order to assess the overall importance of a prey category, based on the percentage of
number, frequency and volume, we used the Index of Relative Importance (IRI, Pinkas et al.,
1971).

To test for diet overlap, we employed the MacArthur and Levins’ index $O_{jk}$ (MacArthur and
Levins 1967) in the pgirmess package (Giraudoux 2016); we built null models using the
‘niche_null_model’ function of the EcoSimR package (Gotelli et al., 2015) to test for statistical
significance of $O_{jk}$. We also assessed prey availability for each site across both dry and wet
seasons, using the Simpson’s diversity index (Supplemental Information 1). We determined
electivity of terrestrial invertebrate prey by the anurans, using the Relativized Electivity Index
(Vanderploeg & Scavia 1979). Following Measey (1998), we computed electivity for only those
prey taxa with $n \geq 10$ prey items for $H. \ tigerinus$ and $Limnonectes$; given the low sample size for
$Fejervarya$ (Table 1), we fixed the cut-off at $n \geq 5$. Further, electivity for $H. \ tigerinus$ was
calculated only for agriculture and plantations; electivity for $Fejervarya$ was considered only for
one site with adequate sample size: Wandoor (Table 1). All analyses were carried out in the
statistical software R 3.4.1 (R Core Team 2017).

RESULTS
Overall, we sampled 798 individuals of the two native anurans and the invasive *Hoplobatrachus tigerinus* (Table 1). We obtained 1478 prey items (*H. tigerinus*: 687, *Limnonectes*: 618, *Fejervarya*: 173) belonging to 35 taxonomic categories in the stomach of 688 anurans (Table 2, Supplemental Information 2). Vacuity index (i.e. proportion of empty stomachs) was higher in the dry season (19.68%) as compared to the wet season (8.67%). Less than 4% of prey items remained unidentified, mostly due to advanced levels of digestion. *Hoplobatrachus tigerinus* consumed prey items under most of the taxonomic categories (29), followed by *Limnonectes* (25), and *Fejervarya* (14). Vertebrates were consumed by both *H. tigerinus* and *Limnonectes*, although the numeric and volumetric percentage of vertebrates consumed was higher for *H. tigerinus* (2.62%, 58.03%) than *Limnonectes* (0.48%, 5.16%; Table 2). Based on IRI, coleopterans and orthopterans constituted the major prey of *H. tigerinus* and *Limnonectes*, whereas, formicids and coleopterans formed the majority in the diet of *Fejervarya* (Table 2).

The diet of *H. tigerinus* overlapped significantly with that of *Limnonectes* (*Ojk* = 0.87, lower-tail $p > 0.999$, upper-tail $p < 0.001$) but there was no significant overlap with *Fejervarya* (*Ojk* = 0.35, lower-tail $p = 0.919$, upper-tail $p = 0.08$). The diet of the two native anurans overlapped significantly (*Ojk* = 0.58, lower-tail $p = 0.967$, upper-tail $p = 0.03$).

Based on availability of terrestrial invertebrates, prey electivity of all three anurans indicated a positive relationship between predator-prey body sizes (Fig. 3). While the largest species, *H. tigerinus*, strongly selected larger prey ($\geq 100$ mm$^3$), the smallest anuran, *Fejervarya*, selected for prey items smaller than 10 mm$^3$; the medium sized *Limnonectes* chose small and medium-sized prey items (10 mm$^3$ – 500 mm$^3$), although the magnitude of electivity (positive or
negative) was lowest for this species (Fig. 1; Fig. 3). We found a positive correlation between prey volume and body size of *H. tigerinus* (β = 1.93, SE = 0.21, p < 0.001) and *Limnonectes* (β = 0.88, SE = 0.25, p < 0.001), but found no such relationship in case of *Fejervarya* (β = -0.07, SE = 0.33, p = 0.83). The majority of prey consumed by the three anurans was hard, and evasive, although diet of *Limnonectes* included a relatively higher proportion of soft and sedentary prey (Table 3). Terrestrial prey were the dominant type in the diet of *H. tigerinus* (91.29%), *Limnonectes* (93.18%), and *Fejervarya* (99.34%).

We observed several endemic vertebrate species in the diet of *H. tigerinus*, including the Andaman emerald gecko *Phelsuma andamanensis* (n = 1), Chakrapani’s narrow mouthed frog *Microhyla chakrapani* (2), the Andaman skink *Eutropis andamanensis* (1), and Oates’s blind snake *Typhlops oatesii* (3). We also found *Limnonectes* (4), unidentified rodent (1), *Lycodon* sp. (1) and the invasive *Calotes versicolor* (3) in the diet of *H. tigerinus* (Supplemental Information 2). *Limnonectes* preyed upon a conspecific on one occasion and an unidentified anuran in another instance.

**DISCUSSION**

We expected the diet of invasive *Hoplobatrachus tigerinus* to overlap significantly with the diet of the two native anurans considered. However, we found a significant overlap only with *Limnonectes*, such that when prey is limited competition may arise. As expected, small vertebrates constituted a majority of *H. tigerinus* diet by volume, suggesting potential impact by predation on a large proportion of the endemic island fauna. Volume of prey elected was
positively related to predator size (Fig. 3); within species, volume of prey consumed was positively correlated with predator size for *H. tigerinus* and *Limnonectes* only. We observed 86% niche overlap between *H. tigerinus* and *Limnonectes*, which was statistically significant in comparison to the constructed null model; whereas, niche overlap of *H. tigerinus* with *Fejervarya* was not significant. On the other hand, prey electivity suggests that *H. tigerinus* strongly elected for medium-sized and larger prey whereas small and medium-sized prey were elected by *Limnonectes* (Fig. 3). This may result in competition for prey ranging from 10 – 500 mm$^3$ between the two anurans, under the conditions of limited prey. Trophic competition in amphibians may lead to a decrease in fitness (e.g. growth rate) and affect population level processes (Benard & Maher, 2011). Impact of invasive amphibians (post-metamorphic) via trophic competition has been documented in fewer studies as compared to predation (Measey et al., 2016), but this mechanism may affect taxa at various trophic levels (Smith et al., 2016). Metamorphs of *H. tigerinus* may also compete with both *Fejervarya* and *Limnonectes* as they would fall under the same size class (20 mm-60mm; Daniels, 2005). The observed positive correlation between body size and prey volume in the case of both *H. tigerinus* and *Limnonectes*, also supports the notion that metamorphs of these species may compete for small prey. Although our sampling did not evaluate the diet of *H. tigerinus* metamorphs, we think this may be relevant as competition between juvenile *Lithobates catesbeianus* and small native anurans has been previously documented on Daishan Island, China (Wu et al., 2005). Evaluating dietary overlap is a pre-cursor to determining trophic competition due to invasive populations, which do not have shared evolutionary history with native species. Dietary overlap
in co-occurring species may be independently influenced by prey availability (Kuzmin, 1995), prey taxa (Lima, 1998), prey size (Toft, 1981; Vignoli et al., 2009; Crnobrnja-Isailović, 2012) and a combination of these factors. Therefore, it is essential to design studies and interpret dietary patterns with reference to all three factors, in order to arrive at meaningful inferences on prey consumed, dietary overlap, and probable subsequent competition (Kuzmin, 1990; but see Kuzmin, 1995 regarding criteria for competition). Further, prey size should ideally be measured in terms of volume, as it is known to be a better dietary descriptor (Vignoli & Luiselli 2012).

Hoplobatrachus tigerinus preyed upon three classes of vertebrates (Amphibia, Reptilia, and Mammalia), which accounted for a significant proportion of its diet by volume, although vertebrate prey was numerically inferior to invertebrates in the diet. Such major contribution to the volume of prey by vertebrates (despite numerical inferiority) has been observed for Lithobates catesbeianus and Xenopus laevis (Boelter et al., 2012; Vogt et al., 2017); anurophagy may also contribute significantly to the diet of many amphibians (Measey et al., 2015; Courant et al., 2017). We observed several endemic species in the diet of H. tigerinus, which may become threatened if frequently preyed upon. Limnonectes was also consumed by H. tigerinus, thereby, indicating a potential two-pronged impact through predation and competition. However, demographic change (if any) in Limnonectes, due to predation and competition by H. tigerinus, was not evaluated in this study. The invasive H. tigerinus on the Andaman Islands reportedly consume poultry (Manish Chandi pers comm., Mohanty & Measey, in review) and stream fish (NPM unpublished data), resulting in a potential economic impact. We expect the invasive H. tigerinus on Madagascar (Glaw and Vences, 2007) to similarly consume a large
proportion of vertebrates in its diet and consider the invasion to be a threat to the highly
diverse small vertebrates of Madagascar.

Despite the presence of a large portion of vertebrates in the diet of *H. tigerinus*, its trophic
position (consistency of vertebrate prey consumption) can only be ascertained with stable
isotope analyses (Huckembeck et al., 2014). Although, diet analysis of invasive species can
identify vulnerable taxa and confirm at least ‘minimal’ to ‘minor’ levels of impact through
predation and competition (*sensu* Blackburn et al., 2014; Hawkins et al., 2015), such analysis
must be complimented with evidence of trophic level effects to evaluate the degree of impact
(Smith et al., 2016).

The large proportion of ants in the diet of *Fejervarya* does not necessarily prove specialization
for myrmecophagy. Hirai and Matsui (2000) inferred relatively weaker avoidance of ants by
*Glandirana rugosa* as compared to other anurans. Although we found the same pattern for
*Fejervarya* based on prey electivity (*E* = -0.02), it does not prove weak avoidance either. As
social insects, ants may be disproportionately captured in the pitfall traps; therefore, it is
necessary to compliment diet studies on potentially myrmephagous predators with additional
evidence (e. g. cafeteria experiments). *Hoplobatrachus tigerinus* and *Fejervarya* chose evasive
prey, suggesting that these two species are mostly ambush (‘sit and wait’) predators;
*Limnonectes* elected sedentary prey along with other prey types, indicating a combination of
‘active search’ and ‘sit and wait’ foraging (Table 3; Huey & Pianka, 1981; Vanhooydonck et al.,
2007). Generally, soft bodied prey are considered to provide more nutrition by size as
compared to hard prey and therefore, it is hypothesized that species will select soft prey more
often than hard prey, which in turn is dependent on prey availability by season (Measey et al., 2011; Carne & Measey 2013). However, we find that diet does not appear to vary considerably across the seasons and is governed more by size than hardness of prey (Fig. 3; Werner et al., 1995).

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

CONCLUSION

Diet analyses of *Hoplobatrachus tigerinus* confirmed our first hypothesis, i.e. significant predation of *H. tigerinus* on endemic vertebrates (hypothesis 1) and partially supported the second hypothesis of a high diet overlap with native anurans (hypothesis 2) indicating potential competition; overlap was significant only for the large-bodied *Limnonectes*. Given the observed high density of *H. tigerinus* in human modified habitats on the Andaman archipelago (NPM unpublished data), trophic competition and predation by *H. tigerinus* may have a significant impact on native anuran populations in these habitats. Pursuing our additional aim of characterizing anuran foraging modes, we determined the foraging strategy of *H. tigerinus* and *Fejervarya* as ambush foraging (‘sit and wait’) and that of *Limnonectes* to be a combination of ‘active search’ and ‘sit and wait’ foraging. In addition to quantifying the trophic niche of anurans belonging to three genera, we stress the necessity to evaluate prey availability and volume in future studies for meaningful insights into 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.
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

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.
Table 1: 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.

|                | Agriculture | Plantation | Disturbed Forest | Undisturbed Forest |
|----------------|-------------|------------|------------------|-------------------|
|                | dry | wet | dry | wet | dry | wet | dry | wet |
| **H. tigerinus** |     |     |     |     |     |     |     |     |
| 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   |
| **Limnonectes** |     |     |     |     |     |     |     |     |
| 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  |
| **Fejervarya** |     |     |     |     |     |     |     |     |
| 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   |
Table 2 (on next page)

Diet of *Hoplobatrachus tigerinus* (n = 687), *Limnonectes* (n = 618) and *Fejervarya* (n = 173) in three sites on the Andaman archipelago

Diet described in terms of percentage N – prey abundance, V – volume, F – frequency of occurrence in anurans, and IRI – Index of relative importance.
Table 2: Diet of *Hoplobatrachus tigerinus* (n = 687), *Limnonectes* (n = 618) and *Fejervarya* (n = 173), described in terms of percentage N – prey abundance, V – volume, F – frequency of occurrence in anurans, and IRI – Index of relative importance.

| Prey      | *Hoplobatrachus tigerinus* (n = 687) | *Limnonectes* (n = 618) | *Fejervarya* (n = 173) |
|-----------|-------------------------------------|-------------------------|------------------------|
|           | N%  | V%    | F%    | IRI  | N%  | V%    | F%    | IRI  | N%  | V%    | F%    | IRI  |
| Acari     | 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    |      |
| 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 |
| Brachyura | 0.58 | 2.40  | 0.76  | 2.27  | 0.16  | 0.81  | 0.19  | 0.19 | 0     | 0     | 0    | 0    |
| Class          | Rank      | 0.14 | 0.09 | 0.19 | 0.02 | 1.61 | 0.20 | 1.95 | 3.55 | 0   | 0   | 0   | 0   | 0   |
|----------------|-----------|------|------|------|------|------|------|------|------|-----|-----|-----|-----|-----|
| Dermaptera     |           | 0.14 | 0.09 | 0.19 | 0.02 | 1.61 | 0.20 | 1.95 | 3.55 | 0   | 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   | 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   | 0   |
| Geckonidae     |           | 0.14 | 0.45 | 0.19 | 0.11 | 0    | 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   | 0   |
| Lepidoptera    |           | 1.31 | 0.24 | 1.33 | 2.07 | 0.48 | 0.14 | 0.39 | 0.24 | 0   | 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   | 0   |
| Odonata        |           | 0.72 | 0.07 | 0.95 | 0.76 | 0.16 | 0.04 | 0.19 | 0.04 | 0   | 0   | 0   | 0   | 0   |
| Class          | 1.31 | 0.77 | 1.52 | 3.18 | 4.69 | 54.54 | 4.10 | 242.95 | 0    | 0    | 0    | 0    |
|----------------|------|------|------|------|------|-------|------|--------|------|------|------|------|
| Oligochaeta    |      |      |      |      |      |       |      |        |      |      |      |      |
| 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|
| Rodentia       | 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 |
| Gastropoda     | 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    |
Table 3 (on next page)

Prey electivity (E’) of the invasive *Hoplobatrachus tigerinus* and native *Limnonectes* and *Fejervarya* based on prey hardness and motility, in three sites of the Andaman archipelago

Classification of prey hardness and motility following Vanhooydonck et al. (2007). Sampling carried out in four habitat types across two seasons, at three sampling locations on the Andaman Islands.
**Table 3.** Prey electivity ($E'$) of the invasive *Hoplobatrachus tigerinus* and native *Limnonectes* and *Fejervarya* based on prey hardness and motility, following Vanhooydonck et al. (2007).

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

|       | *H. tigerinus* |       | *Limnonectes* |       | *Fejervarya* |
|-------|----------------|-------|---------------|-------|--------------|
|       | dry | wet | dry | wet | dry | wet | dry | wet | dry | wet | dry | wet |
| soft  | -0.10 | -0.31 | sedentary | -0.12 | -0.22 |         |      |     |      |     |     |     |
| medium| 0.80  | -0.07 | medium      | -0.70 | 0.20  |         |      |     |      |     |     |     |
| hard  | -0.59 | 0.32  | evasive     | 0.85  | -0.01 |         |      |     |      |     |     |     |
| soft  | 0.52  | 0.14  | sedentary   | 0.41  | 0.15  |         |      |     |      |     |     |     |
| medium| 0.15  | -0.09 | medium     | -0.46 | -0.11 |         |      |     |      |     |     |     |
| hard  | -0.52 | -0.09 | evasive    | 0.31  | -0.06 |         |      |     |      |     |     |     |
| soft  | 0.14  | -0.18 | sedentary  | 0.01  | -0.33 |         |      |     |      |     |     |     |
| medium| -0.45 | -0.43 | medium    | 0.10  | 0.49  |         |      |     |      |     |     |     |
| hard  | -0.01 | 0.38  | evasive   | -0.34 | -0.45 |         |      |     |      |     |     |     |