Dietary niche breadth of endemic and introduced anurans (Amphibia: Anura) in Lombok, Lesser Sunda Islands—Indonesia

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Abstract. Anurans are important organisms as components of faunal community structure in ecosystems because of their roles as secondary and tertiary consumers in food webs. Anurans are opportunistic organisms that will consume any resources in their habitat. In this study, we dissected thirty-nine specimens of anurans from Museum Universitas Mataram (MUM) reference collection, it consists by three endemic (Ingerophrynus biporcatus, Limnonectes dammarmani and L. kadarsani) and one introduced species (Duttaphrynus melanostictus) of anurans. These reference collections were collected by authors during herpetofauna survey at Pusuk Forest, western Lombok in 2018. Based on stomach content analysis, both endemic and introduced anurans are generalist arthropod predators where hymenoptera, coleoptera, orthoptera and chilopoda are the most important food. In this study, we found positive correlations between body size and dietary niche breadth in which each anuran species has a high overlap of dietary niches. Anurans with large body size have a variety of prey than the small one.

1. Introduction
In feeding ecology studies, body size usually has a positive correlation with home range size [1]. The large body size of fauna usually has a wider foraging area and is expected to have a broader habitat niche. They will encounter a wider variety of prey and opportunity as generalist predators [2]. Although the large animals are generalist predators, they will prioritize the large body size of prey to maximize their energy intake. On the other hand, the other small fauna has a narrower habitat niche and they should be selective predators because they are only able to exploit the small prey which are able to catch and fit with their mouth opening [3].

In evolutionary point of view, the generalist species will have a wide feeding plasticity, it is essential for species adaptation in the changing environment. Whereas the specialist species are susceptible to change. On the other hand, if two species have overlapping dietary niches (sharing one or more resources), competition for their resources is likely. If they use identical resources, they cannot coexist (competitive exclusion principle). This theory will relate the overlap boundary to the limit of the number of species that coexist [4].

Frogs and toads are two groups of anurans that are commonly found in Indonesia. Currently 12 species of anurans have been reported in Lombok, six species of them (Fejervarya cancrivora,
Fejervarya limnocharis, Kaloula baleata, Occidozyga laevis, Polypedates leucomystax, and Hylarana erythraea) are cosmopolitan in South-East Asia, the other five species (Ingerophrynus biporcatus, Limnonectes dammermani, Limnonectes kadarsani, Oreophryne monticola and Papurana florensis) are endemic in Lesser Sunda Islands, and the last one (Duttaphrynus melanostictus) was introduced to Lesser Sunda Islands [5-6].

Anurans are commonly opportunistic foragers and generalist predators. Several anuran species could coexist in one habitat, thus competition for food resources might occur. Anurans are important organisms as components of faunal community structure in ecosystems because of their roles as secondary and tertiary consumers in food webs [7]. Anurans also gave indirect ecosystem services such as disease control and agricultural pest control [8]. Several of them have a high sensitivity to thermal, humidity and/or microclimate exchanges. These characteristics make anurans useful bio-indicators of environmental change [7]. The feeding habits of anurans need to be evaluated for understanding their ecological function and how they could coexist in their habitat. In this study, we measured the percentage of occurrence of each food item with regard to the total of stomach content of three endemic anurans (I. biporcatus, L. dammermani and L. kadarsani) and one introduced anuran (D. melanostictus) inhabiting Pusuk Forest, in western Lombok. This secondary forest is a conservation area of Gyrinops versteegii, an endemic eaglewood species in Indonesia.

2. Materials and Methods

2.1. Collection of anurans dietary

We collected diet data of four anuran species of Museum Universitas Mataram (MUM) reference collection with locality at the eaglewood G. versteegii conservation area in Pusuk Forest, Lembah Sari Village, western Lombok. These specimens have been collected by authors during herpetofauna survey at Pusuk Forest in 2018. Thirty-nine specimens of anurans (represented by nine individuals of D. melanostictus, five individuals of I. biporcatus, 10 individuals of L. dammermani, and 15 individuals of L. kadarsani) have been dissected for stomach content analysis. We removed, sorted, and examined stomach contents using a stereoscopic microscope. We preserved the food items in 70% ethanol and identified prey into the smallest possible taxonomic category [9]. For plant material, we dried it in an oven prior to microscopic examination.

2.2. Data analysis

We measured the composition of stomach content in percentages and calculated the niche breadth of each species using standardized Levin’s Index (BA) [10].

\[
BA = \frac{1}{\sum Pj^2} \quad ; \quad BA = \frac{B - 1}{n - 1}
\]

BA = Levins’ standardized niche breadth
B = Levins’ measure of niche breadth
n = Number of possible resource states
Pj = Proportion of resource in the diet of herpetofauna

The BA ranges from 0 (very specialized) to 1 (generalist) niche breadth. If a species does not forage selectively relative to what is available in the environment and has a wide possible niche (generalist niche breadth), the BA value will be near to 1 and vice versa. In this study, we clustered the values of BA into four categories, first category is very specialized niche breadth if BA value less than or equal to 0.250 (BA ≤ First Quartile or Q1), second category is moderate specialized niche breadth if BA value more than 0.250 to 0.500 (Q1 < BA ≤ Q2), third category is moderate generalized niche breadth if BA value more than 0.500 to 0.750 (Q2 < BA ≤ Q3), and the last category is very generalized niche breadth if BA value more than 0.750 (BA > Q3). We analyzed the distribution of data using the Shapiro-Wilk
test and the correlation between niche breadth and body size (Snout to Vent Length/SVL and Body Weight/ BW) were analyzed using Pearson method (R package ‘ggpubr’ v0.4.0) [11].

We measured the niche overlapping between species using Simplified Morisita Index ($\hat{C}_H$) [10]. This index measures overlap of resource use between two populations, being most easily interpreted as a probability. It varies from 0 (no overlap) to 1 (complete overlap).

$$\hat{C}_H = \frac{2 \sum_{i}^{n} \hat{P}_{ij} \hat{P}_{ik}}{\sum_{i}^{n} \hat{P}_{ij}^2 + \sum_{i}^{n} \hat{P}_{ik}^2}$$

$\hat{C}_H$ = Simplified Morisita Index of overlapping between species $j$ and species $k$

$\hat{P}_{ij}$ = Proportion resource $i$ is of the total resources used by species $j$

$\hat{P}_{ik}$ = Proportion resource $i$ is of the total resources used by species $k$

$n$ = Total number of resource states

3. Results

In this study, we examined four species of anurans with locality from the conservation areas of eaglewood G. versteegii in Pusuk Forest, western Lombok. Three of them (I. biporcatus, L. dammarmani and L. kadarsani) are endemic to Lombok, whereas D. melanostictus is not native. D. melanostictus and I. biporcatus are terrestrial toads (family Bufonidae), while L. dammarmani and L. kadarsani are aquatic frogs (family Dicroglossidae) (Figure 1).

![Figure 1. Amphibians in the Pusuk Forest, Western Lombok. (A) Limnonectes kadarsani; (B) Limnonectes dammarmani/ Dammerman’s Wart Frog; (C) Duttaphrynus melanostictus/ Black-spectacled Toad; (D) Ingerophrynus biporcatus/ Double Crested Toad.](image)

Stomach contents analysis revealed the dominant and most important prey were hymenoptera, coleoptera, orthoptera and chilopods (Table 1). To measure how anurans utilize the food resources of their environment, we calculated the dietary niche breadth each anuran species encountered in Pusuk Forest. The analysis result showed that L. kadarsani was a very generalist arthropod predator with levens’ index values more than a third quartile of niche breadth ranges ($B_A > Q3$). It means this species used more than 75% of resource states in anuran's dietary niche at Pusuk forest. Whereas, the last three
species \((D.\ melanostictus, \ I.\ biporcatus\) and \(L.\ dammermani\)) are moderate generalized niche breadth with levin's index values between second to third quartile of niche breadth ranges \((0.500 < B_A \leq 0.750)\). These anurans used < 75% of resource states in anurans dietary niche (Table 1). Based on Morisita Index values, two amphibian families who have different preference microhabitat, Bufonidae are terrestrially and Dicroglossidae are aquatic microhabitat, all of them showed the high overlapping niche breadth (Table 2). The two biggest species \((L.\ kadarsani\) and \(D.\ melanostictus\)) had the largest similarity of dietary niche breadth, whereas the smallest ones \((L.\ dammermani\) and \(I.\ biporcatus\)) have almost 80% of dietary niche breadth similarity.

Table 1. Stomach contents and Leivns’ Index \((B_A)\) of anurans at Pusuk Forest, western Lombok

| Food Type         | \(D.\ melanostictus\) | \(I.\ biporcatus\) | \(L.\ dammermani\) | \(L.\ kadarsani\) |
|-------------------|------------------------|--------------------|---------------------|-------------------|
| Animalia          | 3.72                   | 7.84               | 9.47                | 9.85              |
| Isoptera          | 3.35                   | 0.00               | 0.00                | 4.52              |
| Dictyoptera       | 8.55                   | 0.00               | 7.35                | 6.22              |
| Lepidoptera larvae| 13.30                  | 14.72              | 10.33               | 15.73             |
| Coleoptera        | 14.79                  | 17.16              | 19.88               | 10.22             |
| Hymenoptera       | 14.32                  | 8.28               | 4.32                | 15.52             |
| Orthoptera        | 5.28                   | 16.6               | 6.06                | 5.66              |
| Diptera           | 3.38                   | 8.30               | 0.00                | 3.25              |
| Arachnida         | 16.60                  | 10.53              | 22.71               | 10.24             |
| Mollusca          | 0.00                   | 0.00               | 0.00                | 2.21              |
| Plant leaves      | 3.45                   | 0.00               | 10.00               | 7.15              |
| Unidentified      | 13.26                  | 16.57              | 9.88                | 9.43              |
| Levin’s Index \((B_A)\) | 0.666                 | 0.572              | 0.552               | 0.782             |

Table 2. Niche Overlap \((C_H)\) of anurans at Pusuk Forest, western Lombok.

| Species           | \(D.\ melanostictus\) | \(I.\ biporcatus\) | \(L.\ dammermani\) | \(L.\ kadarsani\) |
|-------------------|------------------------|--------------------|---------------------|-------------------|
| \(D.\ melanostictus\) | -                     | 0.861              | 0.891               | 0.934             |
| \(I.\ biporcatus\)   | -                     | -                  | 0.794               | 0.827             |
| \(L.\ dammermani\)     | -                     | -                  | -                   | 0.817             |
| \(L.\ kadarsani\)       | -                     | -                  | -                   | -                 |

We also measured the pattern of data distribution and the relationship between body size and dietary niche breadth. The distributional data of SVL, BW and niche breadth are normal distributions with \(p\)-value 0.650, 0.052, and 0.467 respectively. In this study we found a significant positive correlation between dietary niche breadth and body size (Snout to Vent Length and Body Weight) with correlation coefficient \((R)\) in both body size characters are 0.79 and \(P\)-value < 0.05 (Figure 2). This result indicates that the bigger species have higher diversity of prey types than the small ones.
Figure 2. Correlation between body size (SVL and BW) and dietary niche breadth ($B_A$) of anurans in Pusuk Forest for (A) Snout-Vent Length (SVL) and (B) Body Weight/BW. *Limnonectes kadarsani* (Lk); *Limnonectes dammarmani* (Ld); *Duttaphrynus melanostictus* (Dm); *Ingerophrynus biporcatus* (Ib). The shading areas are the confidence interval of the correlation coefficient at 95%.

4. Discussion

In this study, we analyzed the dietary niche breadth of four species of anurans (*D. melanostictus, I. biporcatus, L. dammarmani* and *L. kadarsani*) from western Lombok. *D. melanostictus* is a common and cosmopolitan toad which has a wide distribution from northern Pakistan eastward to Huxley’s line. The existence of this species in the eastern part of the Huxley line is the result of its introduction to Lesser Sunda Islands, Sulawesi, Moluccas and New Guinea [12-13]. Meanwhile, the other toad (*I. biporcatus*) is an endemic species which has a limited distribution in Sumatra, Java, and Lesser Sunda Islands (Bali, Lombok, Sumbawa and Rote) [13-14]. The last two species (*L. dammarmani* and *L. kadarsani*) are endemic frogs in the Lesser Sunda Islands [15-16]. All of these anurans coexist in the Pusuk Protection Forest, western Lombok.

Anuran activity in its habitat consists of sitting and waiting (45%), singing (27%), jumping (18%), swimming (5%), amplexus (3%) and feeding (2%) [17]. Domination of sit-and-wait activity made anurans as opportunistic organisms that will use any resources in their habitat. Their food preference is dependent on diversity of the prey in their habitat [18-20]. Unfortunately, we did not measure the arthropods diversity and abundance in the Pusuk Forest, and it made it difficult to conclude that the dominant arthropod frequencies in the stomach of anurans are the dominant species in the forest. Toft identified two groups of anurans based on their dietary niche breadth, the first group is “ant-specialist predator”. The main diet of anurans in this group is small and slow-moving arthropods such as ants and mites. The other group is “non-ant specialist predator”. The main diet of anurans in this group is large and more mobile arthropods such as orthopterans, coleopterans and chilopods [21]. The stomach contents of anurans in this study were dominated by both slow moving-small arthropods such as ants (hymenoptera) with percentages range between 10.22–19.88% and more mobile-large arthropods such as chilopoda, orthoptera and coleoptera with percentages range between 4.32–22.71%. The percentages of small prey are higher in the stomach of small anurans (*I. biporcatus* and *L. dammarmani*). Although these prey provide little energy, these prey items are common and easily obtained in the forest. It made the energetic costs for obtaining these preys low. Whereas, the bigger anurans (*D. melanostictus* and *L. kadarsani*) have a high percentage of large prey in their stomach...
content. The energetic costs for foraging these preys are higher than the small preys, but these preys are more profitable for survival.

Forests provide sufficiently high diversity of prey and microhabitat types for anurans with aquatic, terrestrial, leaf litter, or arboreal life histories [3]. We presume the availability of arthropods as prey for anurans at each microhabitat in the Pusuk Forest is sufficiently high for each species in the ecosystem to have similar access to resources and low competition between species and individuals. Stomach content analysis showed that the study species of anurans had a high diversity of prey types without a particular group of prey being dominant. We conclude that the anurans studied are generalist predators. This wide diet allows the endemic and introduced anurans in Lombok to attain large populations and thus have ‘least concern conservation status’ in IUCN lists. Although these toads and frogs are very abundant, they face different constraints to population persistence. Limnonectes spp. are aquatic frogs, always found in forested streams in primary and secondary forest. They have low to moderate tolerance of habitat disturbance. Increasing human settlements and tourist infrastructure contribute to ongoing decline in the extent and quality of their habitat, so the population is suspected to be decreasing [15-16]. The other endemic species, I. biporcatus is a terrestrial toad that occurs in lowland forest, degraded forest, and tree plantations, but can also be found around human settlements. Due to their tolerance of habitat modification, the populations of I. biporcatus are stable in Lombok but decreasing on Bali, Java and Sumatra following both of D. melanostictus introduction and loss of their habitat [14]. Whereas, introduced toad, D. melanostictus is very adaptable. Due to their tolerance to a broad range of habitats, this species commonly occurs in urban areas and populations are probably increasing in many areas [12].

Other than arthropods, the stomach contents included a small number of plant leaves. In general, anurans cannot digest plant material because they lack the cellular enzyme [22]. These leaves may be accidentally ingested when anurans eat arthropods in their habitat. High intensity foraging will increase the accumulation of leaf content and this content is consistently present in the stomachs of anurans [3, 23].

In this study, we found a high similarity of dietary niche breadth among the endemic species and the introduced species. This may be because the anurans have been collected in the wet season when diversity and abundance of arthropods may be high [21]. Interspecific competition may have been avoided by differential microhabitat use or time of activity. The wide niche breadth may be also due to high variability of prey and large number of food categories used in these analyses.

According to optimal foraging theory, body size has a positive relationship with geographic range size, trophic level and niche breadth [2, 24]. In this study, we also found a positive correlation between body size and dietary niche breadth in endemic and introduced anurans. Anurans commonly are opportunistic predators, eating insects and other small arthropods. These prey types are relatively abundant in tropical forests and inhabit similar microhabitats as the anurans. Therefore, both small and large species of anurans have a potential access to similar sets of prey items. Individuals from larger species have both wider foraging area and various microhabitats, which makes them find a variety of prey than individuals from smaller species.

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