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Wild diet of the critically endangered mountain chicken (*Leptodactylus fallax*)

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In this study, we provide the most complete review to date of the diet of the critically endangered mountain chicken *Leptodactylus fallax* in the wild, describing for the first time the composition of the diet from Montserrat. To do this we report the results of two studies carried out on Montserrat that investigated *L. fallax* diet based on the content of frog gastrointestinal tracts. We found diets on Montserrat to be similar to that recorded for Dominica, typified by opportunism and catholicity, including a wide range of invertebrate prey (dominated by orthopterans) with some small vertebrates eaten too.

Keywords: amphibian, diet, mountain chicken, Monserrat, Dominica

The mountain chicken *Leptodactylus fallax* is the largest endemic amphibian of the Caribbean, the largest living members of the genus *Leptodactylus* (Kaiser, 1994), and one of the world's largest frogs (Adams et al., 2014). As such, the species is an important part of Caribbean ecosystems, as one of the largest native terrestrial predators on the islands on which it occurs. *Leptodactylus fallax* once occurred across seven Caribbean islands, it has since been extirpated from all but two (Dominica and Montserrat) (Adams et al., 2014; Breuil, 2011; Fa et al., 2013; Kaiser, 1994; Malhotra et al., 2007). *Leptodactylus fallax* was widely distributed on Dominica until the early 2000s when the arrival of the pathogen chytrid fungus *Batrachochytridum dendrobatitis* (*Bd*) caused an epizootic of the disease chytridiomycosis leading to rapid and severe population declines (Adams et al., 2014; Magin, 2004; McIntyre, 2003). On Montserrat, *L. fallax* was restricted to the Central Hills of the island until a series of volcanic eruptions beginning in 1995 reduced the species range (Daltry & Gray, 1998; Adams et al., 2014). This was followed by the arrival of *Bd* in 2009 leading to functional extinction of the species on the island in a matter of months (Garcia et al., 2009; Adams et al., 2014).

The only quantitative study of the diet of *Leptodactylus fallax* in the wild is that of Brooks (1982) based on gastrointestinal tract (GIT) contents data of 397 *L. fallax* collected from December 1965 to December 1966, describing a diet characterised by "opportunism and catholicity of choice..." (p.306, Brooks, 1982). Further dietary studies consist of only anecdotal data describing instances of ophiophagy and consumption of the large theraphosid spider *Cyrtopholis femoralis* (Buley, 2003; Rosa et al., 2013).

In this study we report for the first time dietary data for *Leptodactylus fallax* from Montserrat, detailing the results of (1) a study in 1979-1980 before population declines, and (2) a study carried out during the response to the emergence of *Bd* on the island based on post-mortem data of frogs killed by *Bd*. Combining our data with that from Dominica (Brooks, 1982), we provide the most complete review to date of the wild diet of *L. fallax*. We sampled *Leptodacylus fallax* on Montserrat from May 1979 to August 1980. We acquired *L. fallax* specimens from local hunters in the town of Salem who supplied local restaurants with the species. We purchased fresh specimens at dawn (captured the night before) from hunters at above the asking price at restaurants (averaging $3.50 in 1979 and $5.00 in 1980 per frog).

We sampled 206 specimens in this way. We removed the contents of the GIT of all specimens purchased on a given day and analysed the contents whilst still fresh. It should be noted that this sampling took place prior to major declines in the *L. fallax* population on Montserrat and prior to overharvesting being identified as a potential threat to the species. Such a protocol would not be appropriate or ethical for studying the diet of any threatened species, as this procedure has the potential to increase unsustainable hunting pressure on populations. We also sampled *L. fallax* on Montserrat from 1 March 2009 to 27 April 2009. At this time, the authors G.G. and J.L. were dispatched to Montserrat leading the rapid response team to determine the cause of the mass mortality of *L. fallax* reported by the Montserrat Forestry Department on 14 February 2009 (Garcia et al.,

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2009). This survey determined that the cause of mass mortality was *Bd* (Garcia et al., 2009). We carried out surveys in 14 localities within the known distribution range of *Leptodactylus fallax* on Montserrat. All *L. fallax* we encountered were sampled for veterinary analysis (Garcia et al., 2009). We sampled a total of 349 individuals, of these 124 were dead. We carried out post-mortems on all dead specimens. We removed the contents of the GIT of all specimens that had not begun to decay (N=32), storing the GIT contents of each individual in 75 % ethanol in separate plastic specimen tubes for later analysis.

For both data sets (1970-80 and 2009), we inspected GIT contents under stereomicroscopes and identified all prey items with appropriate taxonomic keys (Barrientos, 1988; Chinery, 1993) down to the lowest possible taxonomic levels (Table 1). We recorded the number of prey items of each taxonomic group (N) in both data sets. For the 1979-80 dietary samples we calculated the volume (V) of each prey category from each *Leptodactylus fallax* specimen by measuring the displacement of water in a graduated cylinder upon insertion of prey remains from the GIT (Hyslop, 1980). In the case of the 2009 dataset, we measured the length of intact prey items from the front of the head to the tip of the abdomen (L) and width at the widest point (W). For partially digested prey items we noted the dimensions and then used the formula proposed by Hirai and Matsui (2001) to calculate L and W. We then calculated the volume of each prey item using the formula proposed by Solé et al. (2009):

$$\text{Volume} = (4\pi/3)(L/2)((W/2)^2)$$

Size (mass or volume) measures represent a more accurate representation of diet than frequency of occurrence data as the latter may over-represent small quantities of prey if the prey is small, and under-represent if the prey is large (Deagle et al., 2007; Schmid & Tucker, 2018). In the data we collected (dataset M1 and M2), volume was used as a size measure, however, in Brooks (1982) study (dataset D) dry weight was used as a measure of size. We directly compare proportional measures of volume and dry mass, referring to both collectively as "size" measures. We also recorded occurence of each prey item (O) as the number of *L. fallax* specimens with given prey category found in the GIT.

Due to the historic nature of the datasets, some data had been lost before analysis could take place and some key aspects of experimentation could not be repeated to make data collection consistent between datasets. As such, GIT contents could not be attributed to individuals, instead only totals of each measure were avalible from each dataset. This limited our use of any informative statistical analysis.

A complete list of all food items found in *Leptodactylus fallax* GITs from the Brooks, 1982 Dominica dataset (D), the 1979-1980 Montserrat dataset (M1), and the 2009 Montserrat dataset (M2) is given in Table 1. The total dataset represents the GIT content of 609 specimens of *L. fallax*, 371 from dataset D, 206 from dataset M1, and 32 from dataset M2.

Leptodactylus fallax diet in the wild is summarised for all datasets in Fig. 1. Diet was dominated by orthopterans (25.3 % by frequency, 42.1 % by size), with Opiliones, myriapods, hymenopterans, gastropods, coleopterans, and vertebrates also constituting core components of the diet (>5 % by frequency and/or size). *Leptodactylus fallax* diet is summarised for each dataset in Figure 2, displaying some variation in frequency (Fig. 2A) and size (Fig. 2B) contribution of different prey categories to overall diet between datasets. There is a greater proportional occurrence of prey items of each category in dataset D compared to M2 in all prey categories except hymenopterans, acariformes, dipterans, and hemipterans (Fig. 2A). This indicates that *L. fallax* sampled in dataset D had a more varied diet compared to those in dataset M2.

Seasonal dietary data for *Leptodactylus fallax* was only recorded for datasets D and M2. Two seasons prevail on Dominica and Montserrat; dry (December-April) and wet (June-October) (Brooks, 1982). May and November are considered transitional months, so data from these months was not utilised. Proportions of prey categories by frequency in diet for each season are displayed in Fig. 3A. Differences between seasons were minor, notably an increase in frequency of orthopterans (28.4 % to 32.4 %) and coleopterans (7.9 % to 14.3 %) from dry to wet season, and a decrease in frequency of Opiliones (24.0 % to 15.9 %) and vertebrates (5.1 % to 1.4 %).

Proportions of prey categories in diet by size (mass and volume) for each season are displayed in Fig. 3B. As with frequency of prey items in diet, size composition of prey items in diet also changed little between seasons, however changes that did happen occurred in different prey categories. Notable changes involved an increase in proportional size contribution of gastropods (9.8 % to 14.6 %), myriapods (6.2 % to 11.7 %), and coleopterans (5.3 % to 9.0 %) from dry to wet season, and a decrease in proportional size contribution of Araneae from 6.3 % to <1 % from dry to wet season.

Our study supports the finding of Brooks (p.306, 1982) that "opportunism and catholicity of choice best describe prey capture for *Leptodactylus fallax*". We add additional dietary data to published datasets on GIT contents, providing the first dietary data from the population on Montserrat.

Given that *L. fallax* is an opportunistic generalist, differences in diet between the datasets are likely a result of differences in abundances and availability of prey items between the different islands and time periods. Differences between the Montserrat datasets could also be a result of ash falls caused by volcanic events between 1995 and 2009. Studies on Montserrat found that arthropod populations declined following ash fall events (Marske et al., 2007). Marske et al. (2007) hypothesized that although arthropod numbers as a whole recover rapidly from ash fall-induced declines, total community structure may be altered in the long-term. As such, ash fall induced changes in prey community structures may explain the shifts in diet observed on Montserrat between 1980 (M1) and 2009 (M2). Alternatively, all frogs in dataset M2 were infected with *Bd*, as such, disease may have influenced diet. Weakened frogs may

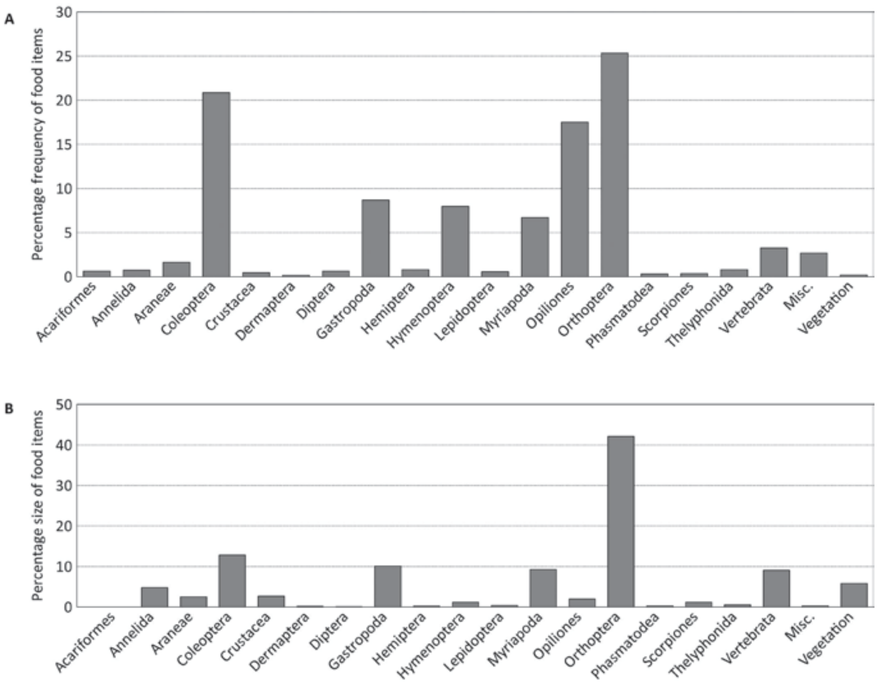

Figure 1. (A) Percentage of total frequency of food items of each prey category, and **(B)** Percentage of total size (proportional volume and proportional dry mass) of food items of each prey category for *L. fallax* across datasets from Dominica (1965-66), and Montserrat (1979-80 and 2009).

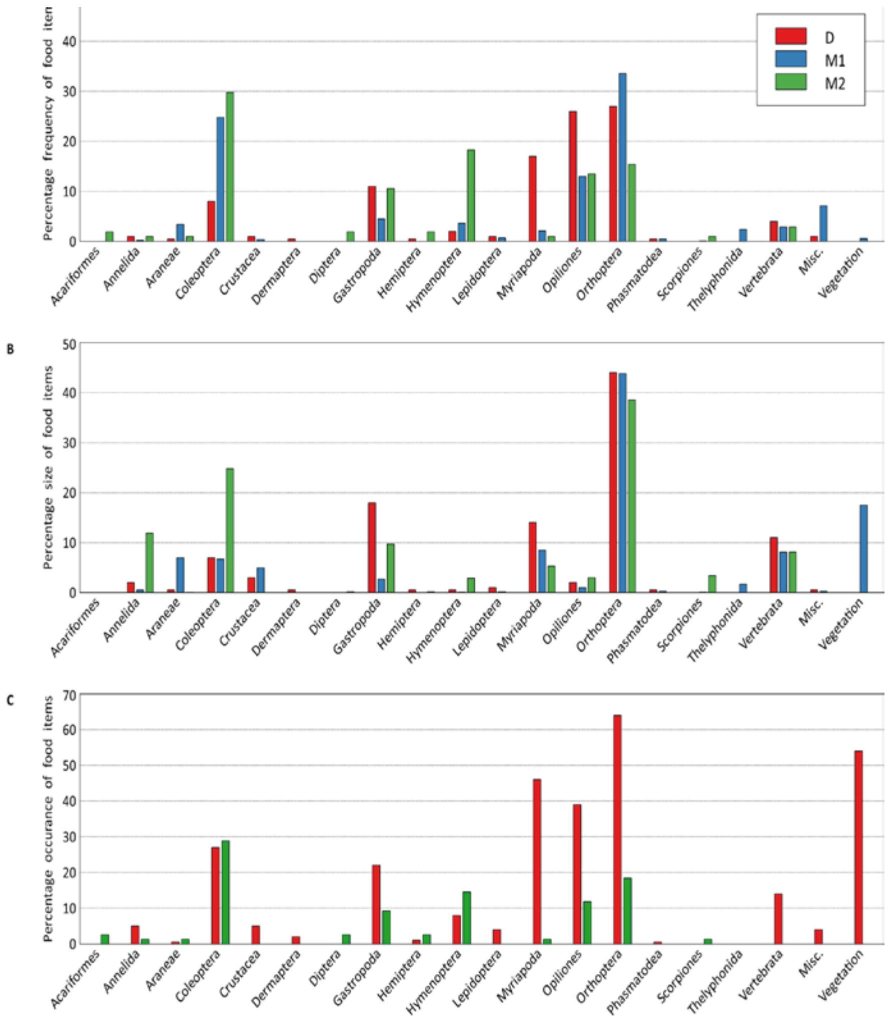

Figure 2. Proportional composition of diet by prey category of *L. fallax* for datasets collected on Dominica 1965-66 **(D)**, and Montserrat 1979-80 (M1)/ 2009 (M2). **(A)** Percentage of total frequency of food items for each prey category. **(B)** Percentage of total size of food items for each prey category (percentage of total dry weight dataset D, percentage of total volume from datasets M1 and M2). **(C)** Percentage of total occurrence of food item per gastrointestinal tract of each prey category.

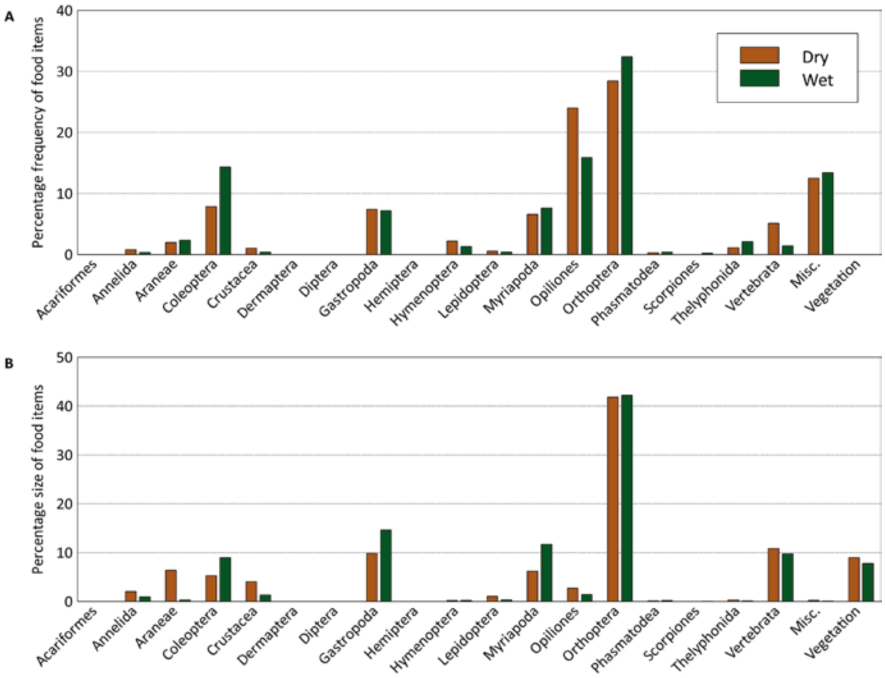

Figure 3. Proportional composition of diet by prey category of *L. fallax* in the dry and wet season by **(A)** percentage of total frequency of food items for each prey category and **(B)** Percentage of total size (percentage of total dry weight dataset D, percentage of total volume from datasets M1 and M2) of food items for each prey category.

Table 1. Percentage of frequency (% N), volume (% V), occurrence (% O), dry mass (% DM), and size (combined DM and V data- % S) for food items of *L. fallax* sampled in Montserrat in 1979-80 (M1) and 2009 (M2), and in Dominica in 1980 (D).

Category/Taxa			M1			M2			D	
	% N	% S	% N	% V	% N	% O	% V	% N	% O	% DM
Acariformes	0.6	<0.1	0	0	1.9	2.6	<0.1	0	0	0
Annelida	0.7	4.8	0.2	0.5	1.0	1.3	11.9	1.0	5.0	2.0
Araneae	1.6	2.5	3.4	7.0	1.0	1.3	<0.1	0.5	0.5	0.5
Coleoptera	20.9	12.8	24.8	6.7	29.8	28.9	24.8	8.0	27.0	7.0
Crustacea	0.5	2.7	0.4	5.0	0	0	0	1.0	5.0	3.0
Dermaptera	0.2	0.2	0	0	0	0	0	0.5	2.0	0.5
Diptera	0.6	<0.1	0	0	1.9	2.6	0.2	0	0	0
Gastropoda	8.7	10.1	4.5	2.7	10.6	9.2	9.7	11.0	22.0	18.0
Hemiptera	0.8	0.2	0	0	1.9	2.6	0.2	0.5	1.0	0.5
Hymenoptera	8.0	1.2	3.6	0.1	18.3	14.5	2.9	2.0	8.0	0.5
Lepidoptera	0.6	0.4	0.7	0.2	0	0	0	1.0	4.0	1.0
Myriapoda	6.7	9.3	2.1	8.5	1.0	1.3	5.3	17.0	46.0	14.0
Opiliones	17.5	2.0	13.0	1.0	13.5	11.8	3.0	26.0	39.0	2.0
Orthoptera	25.3	42.1	33.6	43.8	15.4	18.4	38.5	27.0	64.0	44.0
Phasmatodea	0.3	0.3	0.5	0.3	0	0	0	0.5	0.5	0.5
Scorpiones	0.4	1.2	0.1	0.1	1.0	1.3	3.4	0	0	0
Thelyphonida	0.8	0.6	2.4	1.7	0	0	0	0	0	0
Vertebrata	3.3	9.1	2.9	8.1	2.9	n/a	8.1	4.0	14.0	11.0
Misc.	2.7	0.3	7.1	0.3	0	0	0	1.0	4.0	0.5
Vegetation	0.2	5.8	0.6	17.5	0	0	0	n/a	54.0	n/a

have only been able to consume prey items requiring minimal energetic output to capture and process, leading to a shift in diet compared to that seen in dataset M1.

Seasonal differences in diet for Dominica and Montserrat show the same pattern of changes in prey groups. These changes likely reflect changes in abundance and therefore availability of different prey categories between the wet and dry season (Brooks, 1982) and a change in the size of individuals and/or the presence of different sized species between seasons.

Further long-term studies of diets combined with studies of prey communities would be required to test these hypotheses. We recommend that future studies of amphibian diets incorporate prey community data into their analyses.

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