Received: 3 June 2020 | Revised: 3 August 2020 | Accepted: 19 September 2020

DOI: 10.1111/aje.12814

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ORIGINAL ARTICLE

African Journal of Ecology WILEY

Toad-kill: Prey diversity and preference of invasive guttural toads (*Sclerophrys gutturalis*) in Mauritius

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Funding information
Centre for Collaboration in Africa; DSI-NRF Centre of Excellence for Invasion Biology

Abstract

The invertebrate communities of Mauritius host a high degree of endemism, but are also imperilled by an array of factors, including invasive predators. Since their introduction in 1922, guttural toads (***Sclerophrys gutturalis***) have spread across the island and have been implicated in the decline of a number of endemic invertebrate species. In this study, we examined the feeding habits of the invasive population of guttural toads from three naturally forested locations in Mauritius across multiple years by analysing their stomach content. We also measured the relative abundance of prey items on the landscape using pitfall traps and applied these data to determine prey preference using a Relativised Electivity Index. Insects, malacostracans and gastropods constituted the bulk of the toads' diet (48.7%, 33.4% and 11.8%, respectively), which also included several rare and endemic species. We further determined that insects and malacostracans were also the two most favoured prey taxa, relative to what was available on the landscape. Our investigation has generated several recommendations for future research and provides a fundamental understanding of the diet of guttural toads in the native forests of Mauritius.

KEYWORDS

anuran, conservation, diet, gastropod, invasion biology, invertebrate, Mauritius, predation

Résumé

Les communautés d'invertébrés de l'île Maurice présentent un taux d'endémisme élevé, mais sont également menacées par une multitude de facteurs, notamment des prédateurs envahissants. Depuis leur introduction en 1922, les crapauds gutturaux (*Sclerophrys gutturalis*) se sont répandus à travers l'île et ont joué un rôle dans le déclin d'un certain nombre d'espèces endémiques d'invertébrés. Dans cette étude, nous avons examiné les habitudes alimentaires de la population invasive de crapauds gutturaux au sein de trois sites naturellement boisés situés à l'île Maurice sur plusieurs années en analysant le contenu de leur estomac. Nous avons également quantifié l'abondance relative des proies dans l'environnement à l'aide de pièges à fosse et avons appliqué ces données pour déterminer la préférence en termes de proies à l'aide d'un indice d'électivité relativisé. Les insectes, les malacostracés et les

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gastéropodes constituaient l'essentiel du régime alimentaire des crapauds (respectivement 48,7%, 33,4% et 11,8%), qui comprenait également plusieurs espèces rares et endémiques. Nous avons en outre déterminé que les insectes et les malacostracés étaient également les deux taxons de proies préférés par rapport aux autres proies disponibles dans cet environnement. Notre enquête a généré plusieurs recommandations pour les futures recherches et fournit une compréhension fondamentale du régime alimentaire des crapauds gutturaux dans les forêts indigènes de l'île Maurice.

1 | INTRODUCTION

A major factor contributing to the global decline in biodiversity is the spread of invasive species (Clavero & García-Berthou, 2005; Mooney & Cleland, 2001; Novacek & Cleland, 2001), often due to the negative impacts that they have on native populations and ecosystems (Simberloff et al., 2013). The rate of new introductions of non-native species has shown no signs of decline (Seebens et al., 2017), and invasive species pose particular threats to island ecosystems (Donlan & Wilcox, 2008; Medina et al., 2011; Reaser et al., 2007). The mechanisms by which invasive species cause ecological disruption are multifaceted, with numerous direct (e.g. predation and competition; Greenlees et al., 2006; Mooney & Cleland, 2001; Smith & Quin, 1996) and indirect effects (e.g. altered biotic-relationships; Callaway et al., 2004; Preston et al., 2012). To examine this, invasion biologists can take a community ecology approach to understand the complex relationships and interactions between native and non-native species (Shea & Chesson, 2002). Several invasion hypotheses have been proposed to explain the ramifications of invasions by multiple species and how the interactions within and between native and invasive species either promote or limit invasion success (Catford et al., 2009; Crawley et al., 1999; Eppinga et al., 2006; Simberloff & Holle, 1999). Yet, the foundations of many of these hypotheses rely on the existence of fundamental natural history information and a knowledge on where in a food web a given invader exists, including information on diet, prey preferences and the composition of native/invasive prey.

Biological invasions by anurans (frogs) have resulted in widespread negative ecological, economic and social impacts (Kraus, 2015; Kumschick et al., 2017; Measey et al., 2016; Shine, 2010). However, of the ~147 species of known alien frogs, only four species (cane toads, *Rhinella marina*; American bullfrogs, *Lithobates catesbeianus*; African clawed frogs, *Xenopus laevis*; and coquí frogs, *Eleutherodactylus coqui*) represent the bulk of the research on the topic, with studies on cane toads making up over half of the total literature (van Wilgen et al., 2018). With such a dearth in our understanding of many of the world's invasive frogs, we have significantly limited our ability to properly understand the theoretical and functional mechanisms underpinning anuran invasion success and the role ecological interactions play. As such, there is a clear need to bolster our understanding of the basic ecological effects of understudied invasive species.

The long-standing persistence of guttural toads (*Sclerophrys gutturalis*) in Mauritius represents one such understudied invasive population with an identified need for ecological studies to be undertaken (Kumschick et al., 2017; Measey et al., 2020). Guttural toads were introduced to Mauritius as biocontrol agents for insect pests in 1922 and became invasive shortly thereafter (Cheke, 2010; Cheke & Hume, 2008; Owadally & Lambert, 1988). The native Mauritian ecosystem has no recent shared evolutionary history with anurans. An alien species of ridged frog (*Ptychadena mascareniensis*) and guttural toads represent the only two amphibian species on the island (Cheke & Hume, 2008), both of which are invasive. Furthermore, the Mascarene Islands, comprised of Mauritius, Réunion and Rodrigues, are home to a host of endemic invertebrates such as arachnids (~37% endemic), diplopods (~50%), gastropods (~95%), insects (~37%) and malacostracans (~30%; conservatively estimated from Griffiths & Florens, 2006; Motala et al., 2007; Nentwig et al., 2019). The presence of guttural toads in Mauritius has been suggested to be a contributing factor leading to the declines and extinctions of several endemic native gastropods (Cheke, 2010; Cheke & Hume, 2008; Mauremootoo, 2003), as well as the decline of some carabid beetles (Motala et al., 2007; Vinson, 1935). Recent evaluations of the ecological impacts of invasive amphibians have identified that guttural toads pose a moderate impact to Mauritian invertebrates (within the Environmental Impact Classification for Alien Taxa (EICAT) framework; see Measey et al., 2016; Kumschick et al., 2017), although these assessments came with low confidence scores due to a lack of fundamental dietary data Measey et al., 2020).

Here, we present a formal examination of the diet of guttural toads within their invasive range in Mauritius. Using data sets from two student-led projects, we determine the prey diversity and abundance of the toad's diet—with particular attention being given to gastropod composition (native/invasive species and conservation status), owing to its exceptionally high degree of endemism (Griffiths & Florens, 2006). Collections were conducted across three native forest sites located in protected areas during two sampling periods (2005 and 2017–2018; corresponding with the students' study years). We also examine prey preference by conducting electivity analysis to determine what types of prey items the toads are consuming relative to the prey's abundance on the landscape (a proxy for what is available to toads) and thus determine what prey items are favoured or avoided. Although dietary

and prey preference studies alone do not provide enough insight to determine whether an invasive predator is driving a particular native taxon's decline, they can shed light on the feeding habits of widespread and highly abundant predators—like guttural toads. If these toads are frequently, or preferentially, feeding on a particular imperilled invertebrate taxon, this would give credence to the assertion that these toads could be contributing to biodiversity declines (Cheke & Hume, 2008; Mauremootoo, 2003; Motala et al., 2007; Vinson, 1935).

2 | MATERIALS AND METHODS

2.1 | Study species

Guttural toads have a wide native distribution across large sections of east and southern Africa, excluding arid regions in Botswana, Namibia and western South Africa, and with invasive populations in Mauritius, Réunion and near Cape Town in South Africa (Measey et al., 2017; Measey et al., 2020; Telford et al., 2019; Figure 1). Recently, molecular studies have shown that all three invasive populations originated near the port city of Durban, within the species native range in South Africa (Telford et al., 2019). In their native range, they are a large Bufonid, up to 140 mm SVL, with an opportunistic generalist diet, including a wide variety of invertebrate prey, as well as small lizards and frogs (Channing, 2001; du Preez et al., 2004; Wager, 1986). Since their introduction to Mauritius in 1922, in a failed attempt to control cane beetles (*Phyllophaga smithi*; Cheke & Hume, 2008), the toads spread across the island and can now be found in most habitat types (i.e. agricultural, rural, urban and protected forests; Figure 2).

2.2 | Study sites

We collected data for this study during two sampling periods associated with two student-led research projects. The first in November and December 2005 (n = 146 toads) and the second

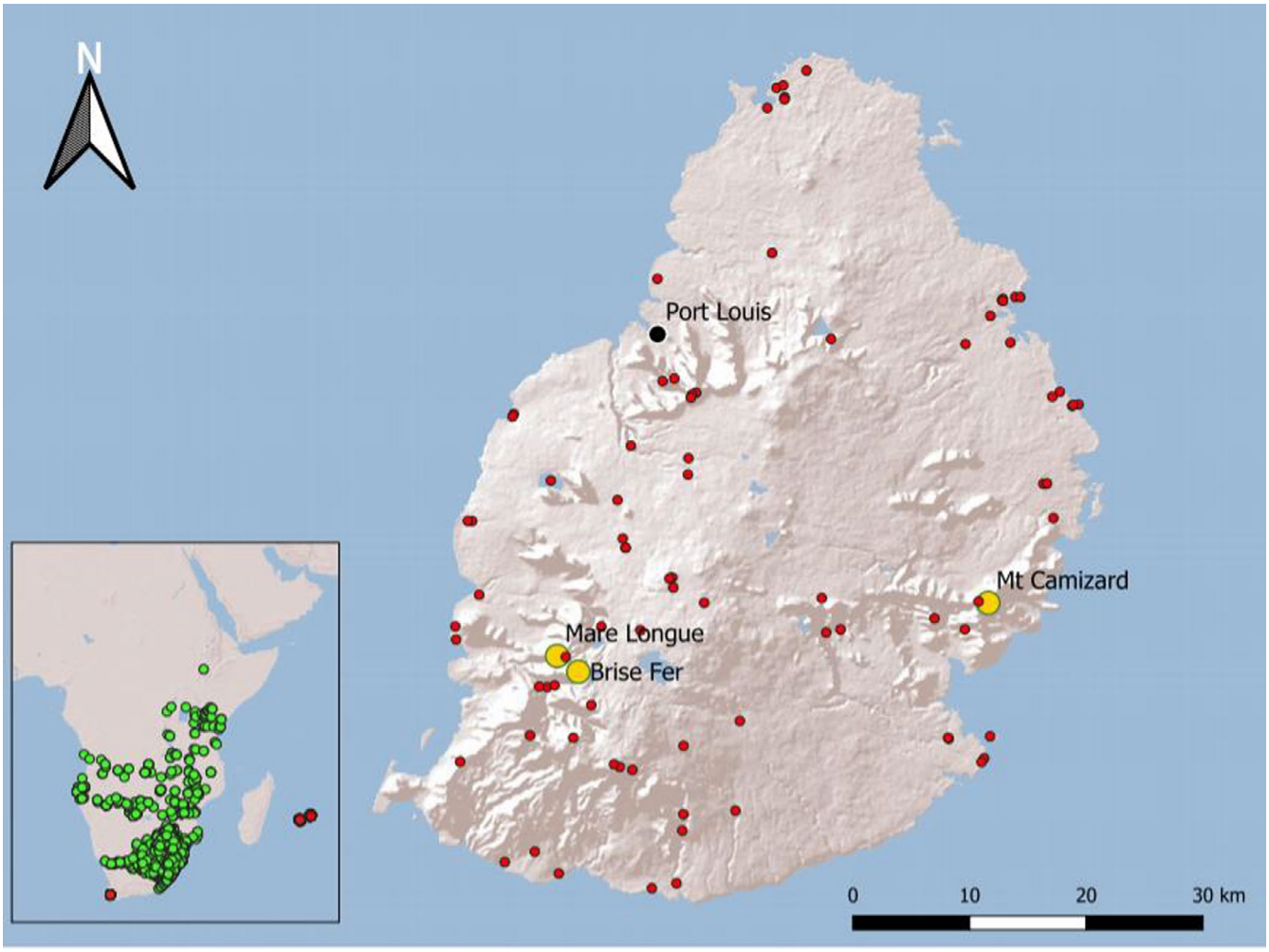

FIGURE 1 The island of Mauritius with the sampling locations of guttural toads (*Sclerophrys gutturalis*) in Brise Fer, Mare Longue and Mont Camizard forests (yellow circles). Known locations of guttural toads are shown as small red circles (J. Measey et al., unpubl.). Inset shows known localities of Guttural Toads in their native (green circles) and invasive (small red circles) ranges

FIGURE 2 A guttural toad (*Sclerophrys gutturalis*) on the Brise Fer forest floor in Black River Gorges National Park, Mauritius

between October 2017 to March 2018 (n = 215 toads). Sampling was conducted at three sites in the protected forests of Brise Fer (2005 and 2017–2018), Mare Longue (2005) and Mont Camizard (2017–2018). All three sites are associated with some of the last remaining native forests in Mauritius (4.4%; Hammond et al., 2015), though they are threatened by the spread of alien plants (Florens et al., 2016). Brise Fer is an evergreen wet native forest occurring at an elevation of 550–600 m and within Black River Gorges National Park in southwestern Mauritius (centred on 20.37°S, 57.44°E; Figure 1). Brise Fer receives a mean annual rainfall of 2,400 mm (Williame, 1984) with mean annual temperatures of 20°C (Padya, 1989) and has a canopy height reaching 20 m (Vaughan & Wiehe, 1937). The area has been under protection as a National Park since 1994 and as a Nature Reserve before that, begining in 1944. Sections of the Brise Fer forest have undergone several alien vegetation removal programmes beginning in 1986 (Florens et al., 1998) and continuing over the last 34 years in an attempt to conserve and protect the native ecosystem. The Mare Longue forest, although only about 2 km Southeast from Brise Fer (centred on 20.38°S, 57.45°E; Figure 1), receives higher rainfall (2,800 mm annually; Williame, 1984) and is located 590–620 m above sea-level. Mare Longue also has an area which has been part of the alien vegetation removal programme operating since 1994. The Mont Camizard forest is also an evergreen wet forest, with a canopy reaching 15–20 m in height (Florens et al., 2012), and is located on the windward slope of the southeast side of Mauritius (centred on 20.33°S, 57.73°E; Figure 1) at an elevation of 315–365 m. It receives a mean annual rainfall of 2,500 mm (Padya, 1984), similar to that of Brise Fer. The Mont Camizard forest has received partial protection against deforestation for at least 375 years under the Mountain Reserves Act of 1983 (Republic of Mauritius, 1984). Similar to the other two sites, the Mont Camizard forest has also had an invasive plant removal programme, beginning in 2005. The removal of the invasive species at all of these sites has resulted in several conservation successes, including the recovery of native butterflies (Florens et al., 2010) and vegetation communities (Baider & Florens, 2011), as well as increased native fruit and flower production (Monty et al., 2013). Restored native forests have also been seen to promote survival in imperilled and endemic land snails (Florens & Baider, 2007); however, they also represent natural areas of Mauritius which continue to be invaded by guttural toads (Motala et al., 2007; Figure 2).

2.3 | Data collection

As part of regional invasive species removal programmes in protected areas, adult toads were haphazardly collected by hand during daytime walking surveys (09:00–16:00 hr). After capture, we measured snout–vent length (SVL) with a set of digital calipers to the nearest mm and then euthanised the toad. During the different sampling periods (2005 and 2017–2018), two euthanasia methods were used on invasive anurans in Mauritius. In 2005, toads were double-pithed, while in 2017–2018 toads were cooled in a refrigerator before being placed in a −20°C freezer (similar to the methods of Lillywhite et al., 2017; Shine et al., 2015, 2019). Once deceased, toads were dissected and preserved in 96% ethanol. The contents of the toad's stomachs were removed, uniquely labelled and preserved in 96% ethanol. We examined stomach contents using a binocular microscope with dietary items grouped by Class (i.e. Arachnida, Clitellata, Diplopoda, Gastropoda, Insecta and Malacostraca). Insects were further identified to the Order level, owing to the wide diversity of functional guilds in this group. Gastropods were further subcategorised to genus or species level (identification conducted by FBVF), in order to ascertain whether they are native or non-native and to provide insights into whether the species being consumed were of notable conservation concern (following Griffiths & Florens, 2006).

To determine the relative abundance of prey items within the landscape, we conducted invertebrate surveys at each of the three locations where toads were collected. Along a set transect at each of the locations and during both sampling periods (2005 and 2017–2018), we placed ten pitfall traps. Each trap consisted of a plastic cup 80 mm in height with a diameter of 65 mm, buried flush with the soil surface and fitted with a plastic plate above the cup approximately 50 mm off the ground to act as a cover preventing rain and leaf litter from entering the trap. The cups were half-filled with antifreeze containing a 50:50 mixture of ethylene glycol and 96% ethanol to kill and preserve invertebrates that entered the trap. We collected each pitfall trap after seven days, and its contents were preserved in 70% ethanol, with its contents then identified to Class (or further for specific groups; see above) and recorded. Unfortunately, we were unable to accurately collect gastropods within the pitfall traps, as they proved rather immune to falling into the traps. Other, less standardised, gastropod surveys were conducted in the area using an active search method (F.B.V. Florens et al., unpubl.), but since this

was not equitably comparable to the pitfall trapping method, we did not include it within the analysis.

2.4 | Statistical analysis

We determined electivity of terrestrial invertebrate prey by the toads, using the Relativised Electivity Index (Vanderploeg & Scavia, 1979), which contrasts the abundance of a given prey category with the toad's stomach content to the abundance of the prey item on the landscape using the pitfall trap data. This metric allows us to estimate whether particular taxa are actively favoured (i.e. positive values), avoided (i.e. negative values) or indiscriminately consumed relative to their abundance in the ecosystem (i.e. a zero value). Following Mohanty and Measey (2018), we computed electivity for only those prey taxa with $n \geq 10$ prey items recovered from the stomach contents and pitfall traps combined. We carried out all analyses in the statistical software R 3.5.1 (R Core Team, 2019).

3 | RESULTS

We collected stomach contents from a total of 361 guttural toads (mean SVL of 48.3 mm ± 0.83 SE; Figure 3) from which we extracted 2,976 prey items (Table 1). We found that the majority of items in the diet of guttural toads from Mauritius' native forests consisted predominantly of insects (n = 1450/2976, 48.7%), malacostracans (n = 993/2976, 33.4%) and gastropods (n = 351/2976, 11.8%; see Figure 4 and Table 1). Of the insects, hymenopterans (predominately ants) were consumed the most (n = 931/1450, 64.2%), with coleopterans (beetles; n = 172/1450, 11.9%), dermapterans (earwigs; n = 112/1450, 7.7%) and hemipterans (true bugs; n = 110/1450, 7.6%) seen as the next three insect Orders eaten in high abundance (Table 1). Although amphipods (terrestrial shrimp) were collected during pitfall trapping, all the malacostracans consumed were isopods (woodlice; n = 993; Table 1). Gastropods made up approximately an eighth of the toad's recorded diet (11.8%; Figure 4). The majority of gastropods recovered from toad stomachs could be identified (336/351; 95.7%) and were native species (n = 293/336; 87.2%), with non-native species making up only 12.8% of the total gastropods consumed (n = 43/336; Table 2). The diversity of gastropod species consumed by invasive guttural toads included 10 species which are Mascarene endemics, of which one has a conservation status listed as Critically Endangered and four as Vulnerable (Griffiths & Florens, 2006; Table 2). However, the majority of native gastropods recovered from guttural toads stomachs is represented by a single species, *Omphalotropis antelmei* (n = 217/293; 74.1%), which is a Mascarene endemic with a conservation status of Least Concern (Griffiths & Florens, 2006; Table 2).

Our Relativised Electivity Index scored malacostrans (0.5), insects (0.4) and clitellate worms (0.3) as preferred prey items, while arachnids (−0.1) and diplopods (−0.8) were avoided (Figure 5). Unfortunately, since gastropods were not accurately reflected within the pitfall trap data, we were unable to determine a Relativised Electivity Index score for this taxon. However, anecdotally it does appear that the ratio of native to invasive gastropods consumed (approximately 7:1) is similar to what is observed on the landscape (F.B.V. Florens et al., unpubl.), suggesting that the toads are not predating either group preferentially.

4 | DISCUSSION

We found that the invasive population of guttural toads in Mauritius had a diverse invertebrate diet and can be seen, much like many other toad species, as a generalist predator (Greenlees et al., 2006; Measey et al., 2015; Razzetti & Msuya, 2002) that will feed on gastropods (Pearson et al., 2009). Despite the broad breadth of prey items, however, ants (Hymenoptera) and woodlice (Isopoda) comprised about 2/3 of the total items recovered from guttural toad stomachs (31.3%, n = 931/2976, and 33.4%, n = 993/2976, respectively), with both of these taxa also representing the two most actively sought prey groups according to our Relativised Electivity Index. The ability to exploit a wide diversity of potential prey items may have aided in the guttural toad's original establishment on the

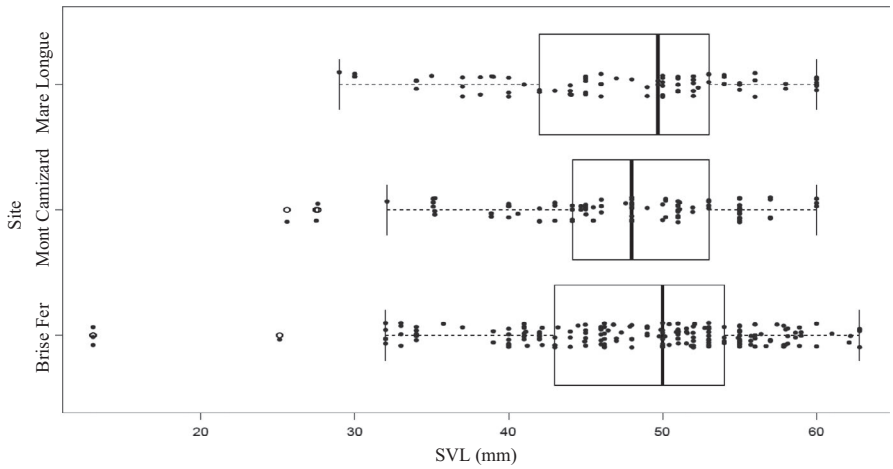

FIGURE 3 Size of guttural toad (*Sclerophrys gutturalis*), measured as snout–vent length (SVL) to the nearest mm, from three sites (see Figure 1) in Mauritius

TABLE 1 Stomach contents for guttural toads (*Sclerophrys gutturalis*) and pitfall trap collection numbers for nongastropod invertebrates (see Table 2) collected in different years in three sites in Mauritius (see Figure 1)

		Brise Fer				Mare Longue		Mont Camizard	
	Year	2005		2017–2018		2005		2017–2018	
	Source	Toad Stomachs	Pitfalls	Toad Stomachs	Pitfalls	Toad Stomachs	Pitfalls	Toad Stomachs	Pitfalls
Class	Order								
Clitellata		0	0	10	6	0	0	3	3
Arachnida	Araneae	62	87	13	67	89	83	3	16
Diplopoda		0	7	1	4	0	4	1	11
Insecta	Blattodea	0	0	1	0	0	0	14	0
	Coleoptera	89	52	23	254	38	28	22	0
	Collembola	9	41	13	11	5	18	0	0
	Dermaptera	90	31	3	53	13	11	6	27
	Diptera	15	55	7	56	17	103	8	38
	Hemiptera	45	21	20	0	41	8	4	0
	Hymenoptera	245	86	85	9	229	86	372	15
	Lepidoptera	0	0	6	0	0	4	5	2
	Orthoptera	7	8	0	0	15	15	1	1
	Phasmida	1	0	0	0	0	0	0	0
	Siphonoptera	0	0	1	0	0	0	0	0
Malacostraca	Isopoda	446	111	15	198	520	107	12	4
	Amphipoda	0	0	0	66	0	0	0	51

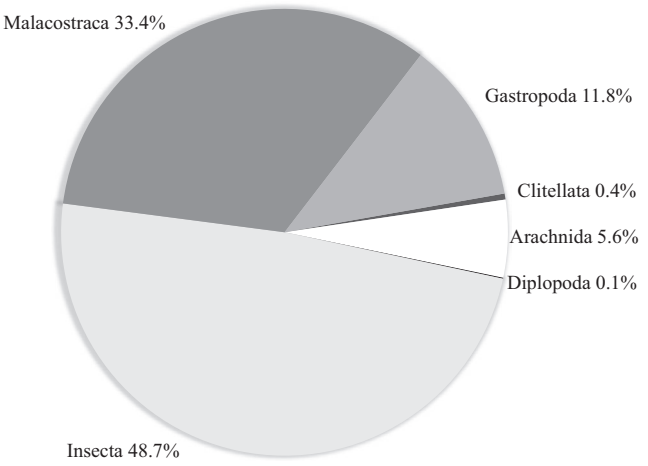

FIGURE 4 The proportion of the total invertebrates (n = 2,976) recovered from the stomach content of guttural toads (Sclerophrys gutturalis) from Mauritius (n = 361), with prey separated by Class (Arachnida, white; Clitellata, deeply dark grey; Diplopoda, black; Gastropoda, grey; Insecta, light grey; Malacostraca, moderately dark grey) and with total per cent values listed beside

island, as opportunistic feeding habits and dietary flexibility has been seen to be advantageous for a host of other invasive taxa (e.g. amphibians, Boland, 2004; earthworms, Zhang et al., 2010; fish, Harms & Turingan, 2012; rodents, Caut et al., 2008; snails, Kwong et al., 2010). Post-establishment, the concentration of their diet on ants and isopods, at least within the upland natural protected areas of Mauritius, may suggest that these toads have been able to capitalise on useful and relatively abundant food sources during their spread across the island. Curiously, the two prey groups, that had previously been identified as threatened by toad predation, native gastropods (Cheke, 2010; Cheke & Hume, 2008; Mauremootoo, 2003) and coleopterans (Motala et al., 2007; Vinson, 1935), were not seen to make up a substantial proportion of the diet, 9.9% (n = 293/2976) and 5.8% (n = 172/2976), respectively.

Understanding the conservation impacts of an invasive predator after almost 100 years of understudied invasion history offers several key challenges. Notably, the prey abundance and diversity are reflective of what species have persisted and thus could skew our ability to understand historical dietary composition and preferences, which may have changed over time. As such, certain native taxa that could have been previously predated upon more heavily at one time may have declined and thus make up less of the toad's contemporary diet. This may be the case for the observation made by Vinson (1935) on the declines of certain carabid beetles which were viewed to correspond with the growing guttural toad population in the 1930s. Scenarios such as this have been seen numerous times, with invasive predators exhibiting tremendous pressure on a specific native species to, or beyond, the brink of collapse, whereby the invader then shifts to a new resource once the prey's population is depleted (Atkinson, 1996; Caut et al., 2008). There are also a host of other invasive predators (e.g. predatory wolfsnails, *Euglandina rosea*; rats, *Rattus* spp.; small Indian mongooses, *Herpestes auropunctatus*; tailess

TABLE 2 The diversity and abundance of gastropods recovered from guttural toad (*Sclerophrys gutturalis*) stomach contents collected in different years at three sites in Mauritius (see Figure 1)

			Brise Fer		Mare Longue	Mont Camizard
		Year	2005	2017–2018	2005	2017–2018
	Status on Mauritius	Conservation Status				
Native Gastropods						
Dancea semifusca	Endemic	Vulnerable			1	
Gonospira callifera	Endemic	Least Concern	3		7	
Louisia barclayi	Native	Least Concern	5			
Maurennea poutrini	Native	Least Concern	2		1	
Microstrophia clavulata	Endemic	Vulnerable			2	
Nesopupa morini	Native	Least Concern	1		1	
Omphalotropis antelmei	Mascarene endemic	Least Concern	80		137	
Omphalotropis clavula	Endemic	Vulnerable			1	
Omphalotropis major	Endemic	Vulnerable	11		2	
Omphalotropis picturata	Mauritius & Réunion Endemic	Least Concern	1			
Omphalotropis plicosa	Endemic	Critically Endangered	1			
Omphalotropis rubens	Mauritius & Réunion Endemic	Least Concern	8		28	
Omphalotropis variegata	Endemic	Least Concern	1			
Alien Gastropods						
Microcystina minima	Non-native	Invasive			1	
Subulina striatella	Non-native	Invasive	11	2	5	4
Subulina octona	Non-native	Invasive		1		
Zonitoides arboreus	Non-native	Invasive	14		5	
Unidentified Gastropods				12		3

Note: Conservation status follows Griffiths and Florens (2006).

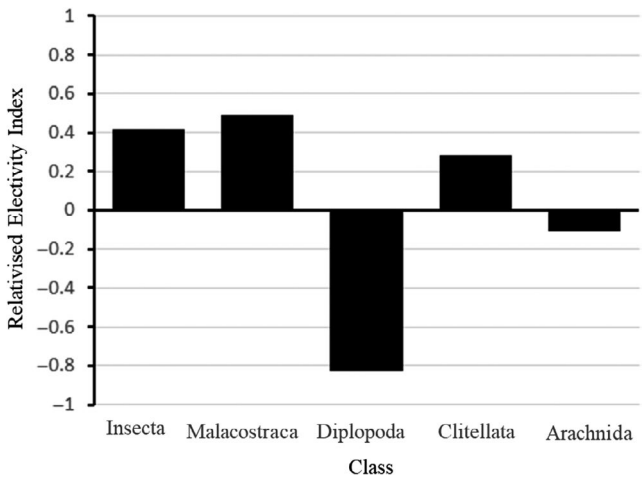

FIGURE 5 Electivity of prey items of guttural toads (*Sclerophrys gutturalis*) pooled across three sites in Mauritius (see Figure 1 and Table 1). Bars above the line are selected in greater proportion than their availability in the environment, while those below the line are underrepresented in stomach contents

tenrecs, *Tenrec ecaudatus*) that likely inflate the level of predation pressure felt by native Mauritian flora and fauna (Cheke, 2010; Cheke & Hume, 2008). Similarly, for species with either historically or currently low populations, any additional mortality threats, even when occurring infrequently, may pose a significant risk. For example, one of the snail species we recovered from a toad stomach, *Omphalotropis plicosa*, is of notable conservation significance as it was presumed extinct until 2002 and has a highly restricted range with seemingly small population sizes (Florens & Baider, 2007; Griffiths & Florens, 2004, 2006). We would suggest that future projects working to conserve imperilled invertebrates in Mauritius, such as *O. plicosa*, should account for guttural toads as a potential threat, even if they only represent a small proportion of the toad's recorded diet. Furthermore, the gastropod species consumed in the highest quantity, *O. antelmei*, is also a Mascarene endemic, and although it has a current conservation status listed as Least Concern (Griffiths & Florens, 2006), there is a clear impetus to maintain its abundance. Therefore, we would recommend future research focus on conservation strategies that could be used to lessen the potential threat posed by toads (e.g. exclusion

of toads from areas of conservation importance) and experimentally determine if removing this predation pressure can result in endemic terrestrial invertebrate population growth.

Beyond determining how the invasion of guttural toads in Mauritius has impacted, or may impact, native species, little is known about how this novel food web has impacted the toads themselves. Previous anecdotal accounts of guttural toads from their native range on mainland Africa have observed that they feed on a wide variety of invertebrate prey, similar to what we observed in Mauritius; however, they have also been seen to consume small vertebrates such as lizards and frogs (Channing, 2001; du Preez et al., 2004; Wager, 1986). Although there are several terrestrial native reptile species present within our study areas, some of notable conservation concern (e.g. Macchabé Skink, *Gongylomorphus bojerii fontenayi*; Bissessur & Florens, 2018), we did not recover any vertebrates within the stomach contents we sampled. By feeding heavily on detritivores (e.g. isopods) and avoiding insectivorous prey (e.g. arachnids, lizards and conspecifics), there is the potential that the toads have shifted their trophic position during their invasion of Mauritius. If a substantial trophic shift has occurred this may help to explain the significant decrease in overall body size (~39% reduction), we observed in Mauritian guttural toads compared to their native source population in Durban (mean SVL 79.2 mm; Vimercati et al., 2018). Both of these postulates (i.e. a functional trophic-level shift and diet-related reduction in body size), however, are speculatory and require further investigation. Unfortunately, to the best of our knowledge there remains no formal examination of the diet and trophic position of guttural toads across their native range, or specifically from the invasive toad's origin population (Durban, South Africa; Telford et al., 2019), from which preliminary comparisons could be made. This presents a fascinating potential avenue for future research to examine how invasions ecologically impact an invader's biology. We hope that our study will spur further comparative investigations of the guttural toad's native diet and trophic position with that of their invasive populations.

Our study follows a similar trend observed with invasive cane toads in Australia, whereby invading toads were seen to actively feed on imperilled invertebrates (i.e. endemic gastropods); however, ecological and environmental factors were expected to vary the toad's direct impact and required further research (Pearson et al., 2009). Here, we present a foundational account of the prey preferences and diversity of invasive guttural toads in Mauritius. Our findings indicated that these toads feed widely on invertebrates, but focus much of their attention on ants and woodlice. Supporting previous accounts of the toads' negative impacts on endemic invertebrates (Cheke & Hume, 2008; Mauremootoo, 2003; Vinson, 1935), we were able to identify several taxa of conservation concern within the toads' stomach contents and advocate for further research to examine these relationships more closely. Additionally, it appears the feeding habits of the invasive guttural toads in Mauritius has the potential to have shifted their trophic level, although more research both within the toad's native and invasive ranges are required. It is important to note, this study only examined individuals from a single habitat type (i.e. protected upland forests) and further dietary investigations into more anthropogenically altered landscapes (e.g. agricultural or urban), and taking into account, other ecological aspects (e.g. density, ontogenetic dietary change, or local carrying capacity) would greatly benefit our understanding of the full scope of the toad's local impact. Overall, with the global numbers of new introductions of non-native species continuing steadily (Seebens et al., 2017) and the ecological and socio-economic impacts of amphibian invasive species becoming more recognised (Measey et al., 2016), there is an incipient need to increased research into the natural history of understudied taxa that are, or have a high likelihood to become, invasive. We hope that our dietary examination will not only prompt further study into applied conservation and management within Mauritius, but also contribute valuable insights from which theoretical invasion biology research can emerge.

ACKNOWLEDGEMENTS

We would like to thank the National Parks and Conservation Service of Mauritius for their support, providing access to toads and locations and approving and permitting our research. We would especially like to thank Mary-Ann Stanley and Owen Griffiths for providing substantial logistical support to enable the data collection as well as access and research permission in Mont Camizard. FBVF, YDP, DSC and CA would like to thank the University of Mauritius for its support. JBG and JM would like to thank the DSI-NRF Centre of Excellence for Invasion Biology and the Centre for Collaboration in Africa at Stellenbosch University for their support.

CONFLICT OF INTEREST

The authors report no conflicts of interest.

DATA AVAILABILITY STATEMENT

All raw data used for this study (i.e. collections from both toad stomachs and pitfall traps) are available and presented in Tables 1 and 2.

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How to cite this article: Baxter-Gilbert J, Florens FBV, Baider C, et al. Toad-kill: Prey diversity and preference of invasive guttural toads (*Sclerophrys gutturalis*) in Mauritius. *Afr J Ecol*. 2020;00:1–10. https://doi.org/10.1111/aje.12814