



Competition and feeding ecology in two sympatric *Xenopus* species (Anura: Pipidae)

Solveig Vogt^{1,2}, F. André de Villiers¹, Flora Ihlow², Dennis Rödder² and John Measey¹

¹Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, Stellenbosch, South Africa

²Herpetology Section, Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany

ABSTRACT

The widespread African clawed frog (*Xenopus laevis*) occurs in sympatry with the IUCN Endangered Cape platanna (*Xenopus gilli*) throughout its entire range in the south-western Cape, South Africa. In order to investigate aspects of the interspecific competition between populations of *X. laevis* and *X. gilli*, an assessment of their niche differentiation was conducted through a comprehensive study on food composition and trophic niche structure at two study sites: the Cape of Good Hope (CoGH) and Kleinmond. A total of 399 stomach contents of *X. laevis* ($n = 183$) and *X. gilli* ($n = 216$) were obtained together with samples of available prey to determine food preferences using the Electivity index (E^*), the Simpson's index of diversity ($1 - D$), the Shannon index (H'), and the Pianka index (O_{jk}). *Xenopus gilli* diet was more diverse than *X. laevis*, particularly in Kleinmond where the Shannon index was nearly double. Both species were found to consume large amounts of tadpoles belonging to different amphibian species, including congeners, with an overall higher incidence of anurophagy than previously recorded. However, *X. laevis* also feeds on adult *X. gilli*, thus representing a direct threat for the latter. While trophic niche overlap was 0.5 for the CoGH, it was almost 1 in Kleinmond, suggesting both species utilise highly congruent trophic niches. Further, subdividing the dataset into three size classes revealed overlap to be higher in small frogs in both study sites. Our study underlines the importance of actively controlling *X. laevis* at sites with *X. gilli* in order to limit competition and predation, which is vital for conservation of the south-western Cape endemic.

Submitted 1 June 2016
Accepted 27 February 2017
Published 19 April 2017

Corresponding author
John Measey, john@measey.com

Academic editor
Donald Kramer

Additional Information and
Declarations can be found on
page 12

DOI 10.7717/peerj.3130

© Copyright
2017 Vogt et al.

Distributed under
Creative Commons CC-BY 4.0

OPEN ACCESS

Subjects Aquaculture, Fisheries and Fish Science, Ecology, Zoology

Keywords Diet, Cannibalism, Alien species, Threatened species, Foraging, Interspecific competition, Trophic niche, Invasive species

INTRODUCTION

Diet and nutrition are widely recognised to represent crucial parameters for understanding life history, population fluctuation, as well as the impact of community modifications (Anderson, Haukos & Anderson, 1999; Dietl, Engels & Solé, 2009). The investigation of species' feeding ecology yields important insights into nutritional requirements as well as into niche segregation in sympatric species (Guidali, Scali & Carettoni, 2000; Leibold

& McPeck, 2006; Knickle & Rose, 2014). If two species overlap in time and space as well as the resources they utilise, and one or more of those resources is limiting, interspecific competition occurs (Begon, Townsend & Harper, 2006; Greenlees et al., 2007). Competition for resources in closely related species has been identified as a driver for speciation and niche segregation (Holt, 1977) which makes the assessment of their feeding ecology a powerful tool to explain interspecific competition (Amundsen et al., 2004). Additionally, interspecific competition between invasives that moved into the ranges of closely related native species is widely accepted to negatively affect populations of the latter (Blackburn et al., 2014).

Among amphibians, invasive populations of the African clawed frog, *Xenopus laevis* (Daudin 1802), have one of the highest recorded impacts of all invasive amphibians (Measey et al., 2016; Kumschick et al., 2017). While the species was originally distributed for pregnancy testing and laboratory use (Gurdon & Hopwood, 2000; Van Sittert & Measey, 2016), today large numbers are exported as pets (Herrel & Van der Meijden, 2014; Measey, in Press). Consequently, invasive populations have established on four continents (Measey et al., 2012 and references therein). While some studies exist on invasive populations (McCoid & Fritts, 1989; Measey, 2001; Lobos & Measey, 2002; Rebelo et al., 2010; Measey, 2016), the autecology of *X. laevis* in its native range in southern Africa is poorly studied and confined to few investigations of diet of populations inhabiting artificial water bodies (e.g., Schoonbee, Prinsloo & Nxiweni, 1992).

Frogs of the family Pipidae are unique among anurans in that they lack a tongue (Ridewood, 1897), whereas feeding modes in all other frogs are usually defined by the pattern of tongue protrusion. Pipids use a unique set of prey capture modes including inertial suction, jaw prehension, forearm scooping, overhead kicks and terrestrial lunges (Avila & Frye, 1978; Measey, 1998a; O'Reilly, Deban & Nishikawa, 2002; Carreño & Nishikawa, 2010). Within the genus *Xenopus*, these feeding modes have been attributed to the capture of different categories of prey, from benthic, planktonic, carrion, nektonic and terrestrial environments (Measey, 1998b; Lobos & Measey, 2002; Bolnick et al., 2003; Amaral & Rebelo, 2012). Despite the potential to consume diverse prey types, including carrion and other frogs (Measey et al., 2015), most studies have revealed zooplankton and benthic invertebrates to constitute the major components of their diet (Kazadi, Bruyn & Hulselmans, 1986; Schoonbee, Prinsloo & Nxiweni, 1992; De Bruyn, Kazadi & Hulselmans, 1996; Bwong & Measey, 2010).

Xenopus laevis is a large pipid (~130 mm SVL in females), and can occur at extremely high densities (>6 per m²; Measey, 2001) causing food resources to become limited (Measey, 1998b). The species has a wide distribution encompassing most of southern Africa, and extending as far north as Malawi (Furman et al., 2015). In contrast, the closely related Cape platanna *Xenopus gilli* Rose and Hewitt, 1927 is much smaller, reaching ~60 mm SVL in females. *Xenopus gilli* is endemic to the south-western Cape of South Africa, and its range is entirely subsumed by *X. laevis* (Picker & De Villiers, 1989; De Villiers, 2004; Fogell, Tolley & Measey, 2013). While *X. laevis* cannot strictly be considered an invasive species in the distribution of *X. gilli*, its numbers are believed to be greatly inflated in the region due to habitat change, specifically the construction of permanent freshwater impoundments (Picker & De Villiers, 1989; De Villiers, De Kock & Measey, 2016), and it has been termed

a ‘domestic exotic’ (Measey *et al.*, 2017). Populations of *X. laevis* have been reported to negatively affect native amphibian communities (Amaral & Rebelo, 2012; Lillo, Faraone & Valvo, 2010; Measey & De Villiers, 2014), with the suggestion that pipids may have a greater proportion of frogs in their diet than all other frogs (Measey *et al.*, 2015). However, its interactions with *X. gilli* in their original habitat remain unclear.

Since its description, there have been concerns about the conservation of *X. gilli*, concentrating on gene introgression through hybridisation with *X. laevis* (Kobel, Pasquier & Tinsley, 1981; Picker, 1985). However, the impact of introgression has been questioned (Evans *et al.*, 1998), and besides habitat change, the greatest threats to *X. gilli* are thought to stem from competition with invading populations of *X. laevis* (Measey, 2011). Several *Xenopus* species are renowned for their cannibalistic tendencies (Measey *et al.*, 2015), and it has been suggested that *X. laevis* can impact populations of *X. gilli* through predation on eggs and tadpoles (Measey, 2011). Picker & De Villiers (1989) suggested that *X. laevis* had competitively excluded *X. gilli* throughout wetland habitats on the Cape Flats. Further evidence that these two *Xenopus* species directly compete comes from the results of removing *X. laevis* in a control programme at the Cape of Good Hope Nature Reserve (CoGH: Picker & De Villiers, 1989). De Villiers, De Kock & Measey (2016) showed that the population of *X. gilli* at CoGH had higher recruitment than those in Kleinmond where *X. laevis* and *X. gilli* occur together at high densities.

In order to investigate the nature of competition between *X. laevis* and sympatric populations of *X. gilli*, we assessed the diet of both species where they occur in sympatry. Niche overlap of the two species was assessed through analyses of prey availability, and the subsequent comparison to stomach contents of adult *X. laevis* and *X. gilli* from two study sites to determine prey selectivity. As predator–prey relations in freshwater environments are particularly size-dependent (Brose *et al.*, 2006), we considered predator size classes within each prey species separately in order to remove the potential for bias from the larger *X. laevis*. Lastly, we assess anurophagy and cannibalism in these natural populations of *Xenopus*.

METHODS

Field research was conducted between July and September 2014 at two study sites, namely, the Cape of Good Hope section of the Table Mountain Nature Reserve (hereafter CoGH) and private land in the vicinity of Kleinmond (hereafter Kleinmond). At both sites, both *Xenopus* species occur sympatrically (Picker & De Villiers, 1989; Evans *et al.*, 1998; Fogell, Tolley & Measey, 2013). At the time of study, the areas were under different management regimes: *X. laevis* were removed annually from CoGH while at Kleinmond they were left (De Villiers, De Kock & Measey, 2016). Both sites consist of a mosaic of permanent impoundments and areas that flood during the austral winter rains (see Table 1). All ponds were visited three days in a row at either two-, or three-week intervals (De Villiers, De Kock & Measey, 2016). Frogs were caught using funnel traps baited with chicken liver contained within a mesh bag to prevent ingestion, set at sunset, and removed within two hours of dawn the following day (approximately 12 h: Measey, 1998b). The majority of dietary samples were obtained by stomach flushing following Measey (1998b). Stomach flushing

Table 1 Locations and sizes of examined water bodies in both study sites in the Western Cape, South Africa.

Site	ID	Coordinates (WGS 1984)	Size (m ²)
CoGH	PP1	34° 18' 21.0" S, 18° 26' 27.4" E	757
	PP2	34° 18' 03.8" S, 18° 26' 30.1" E	946
	PP3	34° 18' 47.5" S, 18° 26' 02.7" E	603
	TP4	34° 18' 43.6" S, 18° 25' 48.1" E	39
	TP5	34° 18' 15.1" S, 18° 26' 27.0" E	48
Kleinmond	TP6	34° 20' 02.4" S, 19° 05' 16.3" E	868
	TP7	34° 19' 48.6" S, 19° 04' 56.1" E	1,514
	TP8	34° 20' 00.1" S, 19° 05' 02.4" E	2,280

Notes.

PP, permanent ponds; TP, temporary ponds.

is a non-lethal method commonly applied to amphibians (*Patto, 1998; Solé et al., 2005*), and no deleterious effects were observed in either species in response to the procedure. Only stomach content samples from *X. laevis* removed from the CoGH were obtained by dissection in the laboratory (*De Villiers, de Kock & Measey, 2016*). All other frogs were released at the site of capture immediately after data collection.

Dietary samples were preserved in 70% ethanol for later examination in the laboratory, where prey items were counted with taxonomic identification to Order level, or lower where possible. It is possible that some prey items flushed from stomachs were ingested within the traps. Therefore, the prey items noted to be attracted to baited traps (i.e., non-*Xenopus* tadpoles and adult pipid frogs), were examined carefully for signs of digestion before inclusion in totals. Ethics approval was granted by Stellenbosch University's Research Ethics Committee: Animal Care and Use (SU-ACUD15-00011). Permission to capture frogs came from CapeNature (AAA007-01867) and South African National Parks (SANParks CRC/2014-2015/001–2009/V1).

In order to assess prey availability, semi-quantitative sampling of potential prey items from the benthos, nekton and zooplankton was conducted at all ponds studied. Samples of the benthic community were collected using a core-tube-sampler (100 cm × 7 cm), and sieved on location through a 2.5 mm mesh. Nektonic organisms were collected through repeated 2 m sweeps using a handheld dip net (2.5 mm mesh), and zooplankton samples were filtered from randomly selected pond water samples (25 l) using a sieve with 0.3 mm mesh. From each pond, we pooled ten core samples, 25 sweeps and three pond water samples to ensure comparative data on prey availability. Samples were subsequently preserved in 70% ethanol for later examination in the laboratory, where prey items were assigned to habitat classes (benthos, nekton, zooplankton and terrestrial), enumerated (N total number of individuals obtained) and their frequency in frogs' stomachs (Freq total number of frogs containing that prey item) with taxonomic identification to Order level, or below. Percentages were calculated on the count for individual taxon compared to the sum for all taxa in that class. The volume of prey items was estimated from linear measures (made using a dissecting microscope and digital callipers to the nearest 0.01 mm) using formulae for geometric shapes (ellipsoid) following *Colli & Zamboni (1999)*.

Data analyses

Studies comparing diversity indices suggest that while common diversity indices appear interchangeable, using several indices provides greater insight into system interactions (Morris *et al.*, 2014). Simpson's index of diversity ($1 - D$) (Simpson, 1949: equation 1) performs best when differentiating between sites; compound diversity measures discriminate because differences are often based on changes in abundant species (Morris *et al.*, 2014); where p is the proportional abundance of resource i .

$$1 - D = \frac{1}{\sum p_i^2}. \quad (1)$$

Simpson's index of diversity ranges from 0 (no diversity) to 1 (high diversity), and was used to measure the diversity of prey items available at different sites. Shannon's diversity (H') is the best index to describe relationships between organisms, such as predator prey relationships (Morris *et al.*, 2014); where p is the proportional abundance of resource i .

$$H' = -\sum p_i^2. \quad (2)$$

In order to determine whether the larger *X. laevis* suppresses the smaller *X. gilli* through interspecific competition for food we quantified the overlap in diet between the sympatric populations using the MacArthur & Levins' index (O_{jk}) (MacArthur & Levins, 1967), as modified by Pianka (1973; equation 3) calculated using the pgirmess package (Giraudeau, 2016) for Cran R 3.1.2 (R Core Team, 2015)

$$O_{jk} = O_{kj} = \frac{\sum_i^n P_{ij} \times P_{ik}}{\sqrt{\sum_i^n P_{ij}^2}} \frac{\sum_i^n P_{ij} \times P_{ik}}{\sqrt{\sum_i^n P_{ij}^2 \times \sum_i^n P_{ik}^2}} \quad (3)$$

where P_{ij} and P_{ik} are the proportions of the i th resource used by the j th and the k th species respectively and n is the number of resource categories. O_{jk} determines dietary overlap between the species pair as ranging from 0 (no overlap) to 1 (complete overlap). Significance of O_{jk} was assessed using a null-model computed with the niche_null_model function of the EcoSim package (Gotelli, Hart & Ellison, 2015) for Cran R. Confidence Intervals calculated refer to the null model (rather than the index) in those cases where the observed O_{jk} is outside of this distribution and the overlap is statistically significant. The same indices were calculated for available prey sampled in the environment (see above). For these measures, all samples were pooled for each site: CoGH and Kleinmond. Food preferences of both *Xenopus* species were assessed using the Electivity index (E^*) (Jacobs, 1974: equation 4)

$$E_i^* = \frac{r_i - p_i}{r_i + p_i - 2r_i p_i} \quad (4)$$

based on the proportions of food category i in the diet (r_i) and in the environment (p_i), which determines electivity ranging from -1 , which indicates total avoidance, to 0 indicating use in proportion to availability, to 1, indicating preference. Following Measey (1998b) electivity was not computed for prey items with a total dietary frequency below 10. Significances of electivity were assessed using Chi-square tests followed by building 95%

Bonferroni confidence intervals (see *Neu, Byers & Peek, 1974; Beyers & Steinhorst, 1984*). Significance was determined at $\alpha = 0.05$.

Predator-prey relations in freshwater environments are highly size-dependent (*Brose et al., 2006*). Because of the pronounced size disparity between the two species (e.g., *Fogell, Tolley & Measey, 2013*), we subdivided the analysis on competition into three size classes for both species: two that cover overlapping size ranges for small (30–52 mm SVL) and medium (52–72 mm), and one for the largest *X. laevis* (>72 mm) (see *Tables S1–S6*) to prevent a potential bias due to the larger body size of *X. laevis*. *Measey (1998b)* suggested that diet of clawed frogs may be influenced by size and sex, making three factors of interest with our primary interest on the difference between species. All statistical analyses and calculations were conducted with Cran R 3.1.2.

RESULTS

A total of 399 stomach contents was collected from both sites, CoGH ($n_{X.laevis} = 94$, $n_{X.gilli} = 111$) and Kleinmond ($n_{X.laevis} = 89$, $n_{X.gilli} = 105$). Less than 2% of all collected prey items could not be identified, mostly because they were too digested or fragmented to be recognised. We identified 21 taxa from stomach content samples of both *Xenopus* species ($n_{X.laevis} = 16$, $n_{X.gilli} = 19$), comprising 12 terrestrial and nine aquatic taxa including eggs, larvae and adult frogs (*Tables 2 and 3*). In addition to these prey items, stomach contents also contained sloughed skin (16%; $n_{X.laevis} = 17$, $n_{X.gilli} = 49$), vegetal matter (14%; $n_{X.laevis} = 34$, $n_{X.gilli} = 23$) and stones ($\sim 1\%$, $n_{X.laevis} = 2$, $n_{X.gilli} = 1$).

Availability of prey items

Simpson's index of diversity ($1 - D$) shows that the diversity of prey items available was more than twice as high in CoGH than in Kleinmond (CoGH: $1 - D = 0.68$; Kleinmond: $1 - D = 0.28$). In the CoGH, by far the most abundant available prey items were zygopterans representing >80% and ostracods representing 6% while all other classes contributed less than 5%. In Kleinmond, anurans (45%), amphipods (29%) and coleopterans (15%) represented the most abundant prey item classes (*Tables 2 and 3*). Aquatic prey appeared in abundance at both sites, with more, smaller prey at the CoGH (mean volume: $24.5 \text{ mm}^3 \pm 2.54 \text{ SE}$) and fewer, larger prey in Kleinmond (mean volume: $60.2 \text{ mm}^3 \pm 7.49 \text{ SE}$) at a ratio of 5:2, respectively.

Interspecific overlap

Shannon's diversity (H') suggests that the diversity of prey consumed at CoGH was very similar between species (H' for *X. laevis* 2.31 and 2.55 for *X. gilli*). In Kleinmond, however, *X. gilli* consumed nearly twice the diversity (H' 2.58) of prey items than those consumed by *X. laevis* (H' 1.64). Niche overlap (O_{jk}) between *X. laevis* and *X. gilli* was 0.491 (95% CI [0.550–0.825], $p_{\text{lower tail}} > 0.999$, $p_{\text{upper tail}} < 0.001$) in the CoGH and 0.965 (95% CI [0.415–0.785], $p_{\text{lower tail}} > 0.999$, $p_{\text{upper tail}} < 0.001$) at Kleinmond. When size classes were analysed separately, niche overlap (O_{jk}) in the CoGH was 0.5 (95% CI [0.010–0.677], $p_{\text{lower tail}} > 0.879$, $p_{\text{upper tail}} < 0.121$) for small and 0.2 (95% CI [0.023–0.840], $p_{\text{lower tail}} > 0.655$, $p_{\text{upper tail}} < 0.345$) for larger frogs while overlap was almost complete for

Table 2 Prey categories consumed by *Xenopus laevis*, *Xenopus gilli* and obtained during habitat sampling at the Cape of Good Hope (CoGH). Consumed sloughed skin, plant matter, and stones not shown for clarity. Prey categories with environmental abundances (Ne, Ne% and Ve) of <1% are shown in grey. N is the total number of individuals obtained in all samples; N% is the percentage of N compared with the total individuals in the entire sample; V is the summed volume of individuals; Freq is the number of stomachs found containing this taxon; E^* is the *Jacobs (1974)* Electivity index; χ^2 = Chi-square residuals, significant values are marked with an asterisk.

CoGH	Environment			<i>Xenopus laevis</i> n = 94						<i>Xenopus gilli</i> n = 111					
	Ne	Ne (%)	Ve	N	N (%)	V	Freq	E^*	χ^2	N	N (%)	Freq	V	E^*	χ^2
Anisoptera	38	1.32	2656.01	27	2.65	1394.94	14	0.34	0.24	11	0.66	6	343.08	-0.34	-2.35*
Brachycera	0	0.00	0.00	3	0.29	56.93	1	1		0	-	-	-		
Coleoptera	9	0.31	8405.49	20	1.96	199.16	11	0.73	6.62*	30	1.79	22	195.34	0.71	11.73*
Ephemeroptera	8	0.28	59.36	0	0.00	0.00	-	-1	-2.37*	3	0.18	3	0.16	-0.22	-0.76
Heteroptera	61	2.12	660.07	15	1.47	152.81	8	-0.18	-4.26*	1	0.06	1	0.70	-0.95	-5.78*
Hymenoptera	0	0.00	0.00	9	0.88	8.15	4	1		3	0.18	3	0.00	1.00	
Nematocera	49	1.71	68.42	65	6.39	19.39	19	0.59	5.54*	23	1.37	15	7.89	-0.11	-0.83
Neuroptera	0	0.00	0.00	1	0.10	0.00	1	1		0	-	-	-		
Psocoptera	1	0.03	0.78	0	0.00	0.00	-	-1	-0.84	0	-	-	-	-1.00	-0.76
Trichoptera	29	1.01	106.48	14	1.38	55.18	7	0.16	-0.53	40	2.39	23	94.52	0.41	6.15*
Zygoptera	2368	82.42	55275.07	24	2.36	390.33	15	-0.99	-0.84	113	6.75	37	1983.17	-0.97	-0.76
Zygentoma	1	0.03	1.41	0	0.00	0.00	-	-1	-40.14*	0	-	-	-	-1.00	-33.94*
Amphipoda	7	0.24	14.26	43	4.22	416.45	10	0.90	24.36*	497	29.71	29	1463.16	0.99	245.74*
<i>Daphnia</i>	98	3.41	139.67	0	0.00	0.00	-	-1	-8.31*	493	29.47	6	91.84	0.84	57.88*
Ostracoda	173	6.02	26.24	586	57.56	88.87	34	0.91	127.9*	352	21.04	25	53.38	0.61	26.84*
Aranae	1	0.03	1.28	0	0.00	0.00	0	-1	-0.84	0	-	-	-	-1.00	-0.76
Acari	13	0.45	0.42	139	13.65	4.61	28	0.94	57.48*	51	3.05	8	1.37	0.75	16.20*
Scorpiones	0	0.00	0.00	0	0.00	0.00	-	-		0	-	-	-		
Anura	17	0.59	3092.02	68	6.71	12368.1	49	0.71	16.2*	24	1.40	22	4365.2	1.00	4.51*

Table 3 Prey categories consumed by *Xenopus laevis*, *Xenopus gilli* and obtained during habitat sampling at Kleinmond. Consumed sloughed skin, plant matter, and stones not shown for clarity. Prey categories with environmental abundances (Ne, Ne% and Ve) of <1% are shown in grey. N is the total number of individuals obtained in all samples; N% is the percentage of N compared with the total individuals in the entire sample; V is the summed volume of individuals; Freq is the number of stomachs found containing this taxon; E^* is the *Jacobs (1974)* Electivity index; χ^2 = Chi-square residuals, significant values are marked with an asterisk.

Kleinmond	Ne	Ne (%)	Ve	N	N (%)	V	Freq	E^*	χ^2	N	N (%)	V	Freq	E^*	χ^2
Blattodea	0	–	–	0	–	–	–			2	0.22	62.38	1		
Brachycera	0	–	–	1	0.06	0.00	1	1		0	–	–	–		
Coleoptera	260	15.09	4.45	65	3.84	1053.55	33	–0.63	–11.62*	123	13.82	1127.53	41	–0.05	0.08
Collembola	0	–	–	0	–	–	–			1	0.11	0.07	1		
Ephemeroptera	9	0.52	0.08	0	–	–	–			0	–	–	–		
Heteroptera	166	9.63	1.16	22	1.30	231.21	11	–0.78	–10.89*	12	1.35	65.84	7	–0.77	–7.64*
Hymenoptera	1	0.06	0.00	0	–	–	–			0	–	–	–		
Nematocera	2	0.12	0.00	9	0.53	5.55	6	0.64	5.06*	14	1.57	113.53	10	0.86	13.23*
Sternorrhyncha	0	–	–	0	–	–	–			1	0.11	0.29	1		
Thysanoptera	0	–	–	0	–	–	–			1	0.11	0.05	1		
Trichoptera	0	–	–	3	0.18	2.08	2			6	0.67	11.29	4		
Zygoptera	0	–	–	1	0.06	24.05	1			0	–	–	–		
Amphipoda	496	28.79	0.93	6	0.35	18.09	6	–0.98	–21.68*	32	3.60	590.05	13	–0.83	–13.45*
<i>Daphnia</i>	1	0.06	0.00	440	25.99	1115.18	4	1.00	445.41*	235	26.40	581.89	15	1.00	336.67*
Ostracoda	0	–	–	1	0.06	0.15	1			23	2.58	3.49	10		
Acari	11	0.64	0.03	1	0.06	1.41	1	–0.83	–2.96*	4	0.45	7.54	3	–0.17	–0.58
Araneae	0	–	–	0	–	–	–	–1	–0.99	1	0.11	0.43	1	1	–0.70
Pseudoscorpiones	1	0.06	0.00	0	–	–	–			–	–	–	–		
Annelida	0	–	–	0	–	–	–			1	0.11	485.36	1		
Anura	776	45.04	93.35	1131	69.32	12692.76	66	1	13.59*	412	47.47	9697.35	63	1	1.83*

both size classes (small 0.92: 95% CI [0.009–0.861], $p_{\text{lower tail}} > 0.999$, $p_{\text{upper tail}} < 0.001$ and large 0.96 95% CI [0.005–0.626], $p_{\text{lower tail}} > 0.997$, $p_{\text{upper tail}} < 0.003$) in Kleinmond.

Anurophagy

In terms of prey frequency, anuran larvae and eggs of various species, including *Xenopus*, were found to represent a major component of the diet of *X. laevis* (67% of all prey items) and *X. gilli* (47% of all prey items; Tables 2 and 3). Subdividing anurans into non-*Xenopus* (eggs, tadpole and adults) and *Xenopus* revealed both *X. laevis* and *X. gilli* feed predominantly on tadpoles of non-*Xenopus* species (CoGH: $N\%_{X. laevis} = 3.35$, $N\%_{X. gilli} = 0.85$; Kleinmond: $N\%_{X. laevis} = 2.48$, $N\%_{X. gilli} = 5.53$). Eggs were also consumed (CoGH: $N\%_{X. laevis} = 0.59$, $N\%_{X. gilli} = 0.37$; Kleinmond: $N\%_{X. laevis} = 0.83$, $N\%_{X. gilli} = 1.50$), while consumption of tadpoles and eggs of *Xenopus* (i.e., potential cannibalism) was negligible ($\text{Freq} < 5$). Considering size classes separately revealed small frogs of both species to feed on non-*Xenopus* tadpoles at both study sites (CoGH: $N\%_{X. laevis} = 3.25$, $N\%_{X. gilli} = 1.00$; Kleinmond: $N\%_{X. laevis} = 2.62$, $N\%_{X. gilli} = 11.01$) which was also true for medium sized frogs in Kleinmond ($N\%_{X. laevis} = 1.83$, $N\%_{X. gilli} = 9.43$).

Adult non-*Xenopus* frogs consumed (all *Cacosternum australis*; SVLs 20.5, 22.7 and 21.2 mm) were found in dietary samples of both *Xenopus* species in Kleinmond, but in the CoGH an *X. laevis* (SVL 79.6 mm) was found to prey on adult *X. gilli* (SVL 36.9 mm). Anurophagy differed greatly between Kleinmond, where the ratio between anurans and total prey was 0.47 for *X. gilli* and 0.67 for *X. laevis*, to much lower levels at the CoGH where the same ratio was 0.01 for both *X. gilli* and *X. laevis*.

DISCUSSION

Previous studies have documented the presence of competition between *Xenopus gilli* and *X. laevis*, evidenced by a reduction in recruitment of *X. gilli* while *X. laevis* increases in abundance (De Villiers, De Kock & Measey, 2016; Picker & De Villiers, 1989). For one aspect of this competition, we show a large dietary niche overlap of ~50% in the Cape of Good Hope reserve and almost complete overlap (97%) in Kleinmond, suggesting a high level of competition for food resources between the two species. Our analysis of prey volume revealed that the larger *X. laevis* are likely to impact greatly on available food items through predation. This information combined with the knowledge that *X. laevis* typically outnumber *X. gilli* around 3:1 (De Villiers, De Kock & Measey, 2016) suggests that competition for finite prey resources is likely to be a serious impediment to the survival of *X. gilli*. Also, we also found direct predation of adult *X. gilli* by *X. laevis*, an interaction previously only speculated (Picker & De Villiers, 1989; Fogell, Tolley & Measey, 2013).

Studies on diet of *Xenopus* species suggest that they do not remain static, but adapt together with prey availability throughout the year (see Measey, 1998b). A study of diet during summer of 1983 in the CoGH showed that the prey consumed in these permanent ponds remains very similar (Simmonds, 1985) to the results we show for winter. Interestingly, Simmonds (1985) recorded many *Xenopus* eggs and larvae in the stomachs, but does not mention the high number of tadpoles of other species that we found. Although Simmonds suggests that consumption of tadpoles could be related to

them being confined in traps, we found that many of those we removed from stomachs were partially digested, suggesting ingestion prior to entering traps. [Measey et al. \(2015\)](#) calculated the proportion of amphibian prey from 355 records of 228 species of anurans, finding that pipids have (on average) the highest proportion of anurans in their diet, while the highest proportion previously recorded in a single study was in *Lithobates catesbeiana* which had an anurophagy proportion of 0.19 ([Leivas, Leivas & Moura, 2012](#)). In this study, *X. laevis* and *X. gilli* in Kleinmond were found to have an anurophagy proportion of 0.67 and 0.47, although these proportions were much lower at CoGH (0.01 for both species). Our data, therefore, shows that the diet of *X. laevis* from Kleinmond comprises three and a half times the proportion of amphibians than any other known adult anuran, confirming the importance of anurophagy for pipids in general and at this site in particular.

Our study determined some differences in diet between sites. At the CoGH, *X. gilli* preys on a large variety of different prey taxa, utilising a wider and more diverse niche than in Kleinmond. While the niche of *X. laevis* was broader at the CoGH it was more diverse in Kleinmond where availability of potential prey items was mainly restricted to anuran eggs and larvae. In addition, consumption of terrestrial prey items was significantly higher in both species in Kleinmond suggesting that the restricted diversity of available aquatic prey induces *Xenopus* to catch terrestrial prey as reported by [Measey \(1998b\)](#). The same author also suggested terrestrial prey might represent an important component of the diet of *X. laevis*, and this might particularly apply to sites with a restricted aquatic food supply. Amounts of terrestrial prey were higher in *X. laevis* than in *X. gilli*, but compared to prevalence of aquatic prey, low at both sites. Aquatic prey was apparently in abundance at both sites, with very few animals having empty stomachs.

Our data suggest that dietary competition is not equal among size classes with increased competition between smaller individuals. This is of note as the larger *X. laevis* is likely to grow faster (see [McCoid & Fritts, 1989](#); [Measey, 2001](#)) and be under this more intense competition for a shorter period of their lives. While our study reveals from a single sampling point how dietary resources are partitioned between these species, competition occurs over the life of individuals. With abundant prey, we show that sympatric *Xenopus* species do have a large dietary overlap, but direct competition for dietary resources may only occur when these resources are limited. Presumably, the ongoing removal of *X. laevis* from the CoGH keeps competition there at a very low level. However, in Kleinmond, not only do *X. laevis* outnumber *X. gilli* at a ratio of 3:1 ([De Villiers, De Kock & Measey, 2016](#)), but sites dry annually which may provoke increased competition as water levels fall. In addition, we do not consider here the competition between larvae, or for other limited resources such as egg deposition locations at either site, although these would be important over the life of individuals.

Food composition observed for *X. laevis* is generally in accordance with earlier studies ([Schoonbee, Prinsloo & Nxiweni, 1992](#); [Measey, 1998b](#); [Lobos & Measey, 2002](#); [Faraone et al., 2008](#); [Lillo, Faraone & Valvo, 2010](#); [Amaral & Rebelo, 2012](#)). While *X. laevis* has previously been reported to negatively affect native amphibian populations ([Crayon, 2005](#); [Rebelo et al., 2010](#); [Lillo, Faraone & Valvo, 2010](#); [Amaral & Rebelo, 2012](#)), by consuming tadpoles and eggs ([Schoonbee, Prinsloo & Nxiweni, 1992](#); [Faraone et al., 2008](#)), here we report them

to prey on adult frogs, including its endangered conspecific *X. gilli*. Thus, *X. laevis* is a direct predator of *X. gilli*. In this study, the other native amphibians consumed included tadpoles of the common Cape River Frog *Amietia fuscigula* and adults and tadpoles of the southern dainty frog *Cacosternum australis*. [Measey & De Villiers \(2014\)](#) previously reported consumption of the clicking stream frog *Strongylopus grayii* at the same site near Kleinmond.

Dietary samples also contained sloughed skin, plant matter and stones, also reported by [Measey \(1998b\)](#), [Faraone et al. \(2008\)](#) and [Amaral & Rebelo \(2012\)](#). However, pipid frogs are known for their inertial suction feeding method ([Sokol, 1969](#)) which likely leads to the accidental ingestion of soil or plant matter. While previous research from South Wales and Sicily ([Measey, 1998b](#); [Faraone et al., 2008](#)) found in the diet of invasive *X. laevis* that zooplanktonic components represent the numerically most abundant prey group, our results partly support this result for both species in the CoGH but suggest that *Xenopus* mainly consume nektonic prey (in terms of volume and frequency). However, benthic organisms represented the numerically most abundant prey for both populations of *X. laevis* from Chile ([Lobos & Measey, 2002](#)).

Neither *Xenopus* species was found to take prey in the same proportion as it occurred in the environment. The low consumption of some abundant prey taxa at each site (e.g., Zygoptera at the CoGH or Amphipoda in Kleinmond) combined with a selection for other taxa (e.g., *Daphnia*, amphibian larvae and eggs) indicates that resource use was not random and not exclusively determined by availability, agreeing with previous assessments ([Measey, 1998b](#)). Thus, both species seem to select similar resources from within the environment. According to [MacArthur & Pianka \(1966\)](#), optimal foragers are typically expected to choose prey according to profitability irrespective of density. However, preferences of both species were not entirely consistent across sampling localities. Handling time for different prey items, especially for predators such as *Xenopus*, which are capable of many different feeding modes, is likely to vary widely. The preference that we observe for zooplankters may represent the very small handling time involved in suction feeding compared to actively swimming and/or lunging after nektonic prey. Ultimately, prey choice may result from a great many factors including individual variation in diet, which has been found in a number of amphibian, fish and some avian species ([Bolnick et al., 2002](#); [Araújo et al., 2008](#); [Thiemann et al., 2011](#); [Schriever & Williams, 2013](#)). This variation is not simply due to different choices of prey taxa, but rather because some animals exhibit very specialised diets, while other individuals are more generalist.

Interspecific competition is an important factor in the structuring of predatory communities ([Caro & Stoner, 2003](#)), usually involving a dominant and an inferior competitor ([Holt, 1977](#); [Rehage, Barnett & Sih, 2005](#); [Harrington et al., 2009](#)). In some competitive interactions, even direct aggression is involved ([Hersteinsson & Macdonald, 1992](#); [Harrington et al., 2009](#)), leading to the death of the inferior competitor ([Palomares & Caro, 1999](#)) or resulting in mutual consumption. Our results agree with the previously demonstrated dominant position of *X. laevis* in the competition with *X. gilli* ([De Villiers, De Kock & Measey, 2016](#)); through increased resource use by larger individuals, and direct predation on *X. gilli* eggs, larvae and adults. Therefore, this study supports the continued

removal of *X. laevis* in the CoGH. The conservation of *X. gilli* in Kleinmond and at other sites will rely on new plans to remove its congeneric competitor, *X. laevis*.

ACKNOWLEDGEMENTS

We would like to thank the staff of SANParks, and in particular Marissa De Kock, and the landowners at Kleinmond for their help and facilitation of this study. The authors kindly thank the reviewers and Donald Kramer for their suggested revisions, which helped improve the manuscript.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

The National Research Foundation (NRF) of South Africa (NRF Grant No. 87759 to GJM) provided financial support. SV, FAdV and JM received financial and logistical support from the DST-NRF Centre of Excellence for Invasion Biology (CIB). This project was conducted in collaboration with the BiodivERsA project “Invasive biology of *Xenopus laevis* in Europe: ecology, impact and predictive models”. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
National Research Foundation (NRF) of South Africa: 87759.
DST-NRF Centre of Excellence for Invasion Biology (CIB).

Competing Interests

John Measey is an Academic Editor for PeerJ. The authors declare there are no competing interests.

Author Contributions

- Solveig Vogt performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- F. André de Villiers performed the experiments, wrote the paper, reviewed drafts of the paper.
- Flora Ihlow analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Dennis Rödder analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper.
- John Measey conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

Stellenbosch University Research Ethics Committee: Animal Care & Use: SU-ACUD15-00011.

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

CapeNature (AAA007-01867) and South African National Parks (SANParks CRC/2014-2015/001–2009/V1).

Data Availability

The following information was supplied regarding data availability:

The raw data has been supplied as a [Supplementary File](#).

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.3130#supplemental-information>.

REFERENCES

- Amaral P, Rebelo R. 2012.** Diet of invasive clawed frog *Xenopus laevis* at Lage stream (Oeiras, W Portugal). *The Herpetological Journal* **22**(3):187–190.
- Amundsen P-A, Knudsen R, Klemetsen A, Kristoffersen R. 2004.** Resource competition and interactive segregation between sympatric whitefish morphs. *Annales Zoologici Fennici* **41**(1):301–307.
- Anderson AM, Haukos DA, Anderson JT. 1999.** Diet composition of three anurans from the Playa Wetlands of Northwest Texas. *Copeia* **1999**:515–520 DOI [10.2307/1447502](https://doi.org/10.2307/1447502).
- Araújo MS, Guimaraes Jr PR, Svanbäck R, Pinheiro A, Guimarães P, Reis SFD, Bolnick DI. 2008.** Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. *Ecology* **89**(7):1981–1993 DOI [10.1890/07-0630.1](https://doi.org/10.1890/07-0630.1).
- Avila VL, Frye PG. 1978.** Feeding behavior of the African clawed frog (*Xenopus laevis* Daudin):(Amphibia, Anura, Pipidae): effect of prey type. *Journal of Herpetology* **12**:391–396 DOI [10.2307/1563621](https://doi.org/10.2307/1563621).
- Begon M, Townsend CR, Harper JL. 2006.** *Ecology: from individuals to ecosystems*. 4th edition. Oxford: Blackwell Publishing.
- Beyers CR, Steinhorst RK. 1984.** Clarification of a technique for analysis of #utilization-availability data. *Journal of Wildlife Management* **48**(3):1050–1053 DOI [10.2307/3801467](https://doi.org/10.2307/3801467).
- Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Nentwig W, Pergl J. 2014.** A unified classification of alien species based on the magnitude of their environmental impacts. *PLOS Biology* **12**(5):e1001850 DOI [10.1371/journal.pbio.1001850](https://doi.org/10.1371/journal.pbio.1001850).
- Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003.** The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* **161**:1–28 DOI [10.1086/343878](https://doi.org/10.1086/343878).

- Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R. 2002.** Measuring individual-level resource specialization. *Ecology* **83**:2936–2941
[DOI 10.1890/0012-9658\(2002\)083\[2936:MILRS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2936:MILRS]2.0.CO;2).
- Brose U, Jonsson T, Berlow EL, Warren P, Banasek-Richter C, Bersier LF, Blanchard JL, Brey T, Carpenter SR, Blandenier MF, Cushing L. 2006.** Consumer-resource body-size relationships in natural food webs. *Ecology* **87**:2411–2417
[DOI 10.1890/0012-9658\(2006\)87\[2411:CBRINF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2).
- Bwong BA, Measey GJ. 2010.** Diet composition of *Xenopus borealis* in Taita Hills: effects of habitat and predator size. *African Journal of Ecology* **48**:299–303
[DOI 10.1111/j.1365-2028.2009.01149.x](https://doi.org/10.1111/j.1365-2028.2009.01149.x).
- Caro T, Stoner C. 2003.** The potential for interspecific competition among African carnivores. *Biological Conservation* **110**:67–75 [DOI 10.1016/S0006-3207\(02\)00177-5](https://doi.org/10.1016/S0006-3207(02)00177-5).
- Carreño CA, Nishikawa KC. 2010.** Aquatic feeding in pipid frogs: the use of suction for prey capture. *The Journal of Experimental Biology* **213**:2001–2008
[DOI 10.1242/jeb.043380](https://doi.org/10.1242/jeb.043380).
- Colli GR, Zamboni DS. 1999.** Ecology of the worm-lizard *Amphisbaena alba* in the Cerrado of Central Brazil. *Copeia* **1999**:733–742 [DOI 10.2307/1447606](https://doi.org/10.2307/1447606).
- Crayon J. 2005.** Species account: *Xenopus laevis*. In: Lannoo MJ, ed. *Amphibian declines: the conservation status of United States species*. Berkeley: University of California Press, 522–525.
- De Bruyn L, Kazadi M, Hulselmans J. 1996.** Diet of *Xenopus fraseri* (Anura, Pipidae). *Journal of Herpetology* **30**:82–85 [DOI 10.2307/1564714](https://doi.org/10.2307/1564714).
- De Villiers A. 2004.** Species account: *Xenopus gilli* (Rose & Hewitt, 1927). In: Minter LR, Burger M, Harrison JA, Bishop PJ, Braack H, eds. *Atlas and red data book of the frogs of South Africa, Lesotho and Swaziland*, Washington, D.C.: Smithsonian Institution Press, 260–263.
- De Villiers FA, De Kock M, Measey GJ. 2016.** Controlling the African clawed frog *Xenopus laevis* to conserve the Cape platanna *Xenopus gilli* in South Africa. *Conservation Evidence* **13**:17.
- Dietl J, Engels W, Solé M. 2009.** Diet and feeding behaviour of the leaf-litter frog *Ischnocnema henselii* (Anura: Brachycephalidae) in Araucaria rain forests on the Serra Geral of Rio Grande do Sul, Brazil. *Journal of Natural History* **43**:1473–1483
[DOI 10.1080/00222930902898709](https://doi.org/10.1080/00222930902898709).
- Evans B, Morales J, Picker M, Melnick DJ, Kelley DB. 1998.** Absence of extensive introgression between *Xenopus gilli* and *Xenopus laevis laevis* (Anura: Pipidae) in southwestern Cape Province, South Africa. *Copeia* **1998**:504–509 [DOI 10.2307/1447452](https://doi.org/10.2307/1447452).
- Faraone FP, Lillo F, Giacalone G, Valvo ML. 2008.** The large invasive population of *Xenopus laevis* in Sicily, Italy. *Amphibia-Reptilia* **29**:405–412
[DOI 10.1163/156853808785112075](https://doi.org/10.1163/156853808785112075).
- Fogell DJ, Tolley KA, Measey GJ. 2013.** Mind the gaps: investigating the cause of the current range disjunction in the Cape Platanna, *Xenopus gilli* (Anura: Pipidae). *PeerJ* **1**:e166 [DOI 10.7717/peerj.166](https://doi.org/10.7717/peerj.166).

- Furman BL, Bewick AJ, Harrison TL, Greenbaum E, Gvoždík V, Kusamba C, Evans BJ. 2015.** Pan-African phylogeography of a model organism, the African clawed frog ‘*Xenopus laevis*’. *Molecular Ecology* **24**:909–925 DOI [10.1111/mec.13076](https://doi.org/10.1111/mec.13076).
- Giraudoux P. 2016.** pgirmess: data analysis in ecology. R package version 1.6.4. Available at <http://CRAN.R-project.org/package=pgirmess>.
- Gotelli NJ, Hart EM, Ellison AM. 2015.** EcoSimR: Null model analysis for ecological data. R package version 0.1.0. Available at <http://github.com/gotellilab/EcoSimR>.
- Greenlees MJ, Brown GP, Webb JK, et al. 2007.** Do invasive cane toads (*Chaunus marinus*) compete with Australian frogs (*Cyclorana australis*)? *Australian Ecology* **32**(8):900–907 DOI [10.1111/j.1442-9993.2007.01778.x](https://doi.org/10.1111/j.1442-9993.2007.01778.x).
- Guidali F, Scali S, Carettoni A. 2000.** Diet and trophic niche overlap of two ranid species in northern Italy. *Italian Journal of Zoology* **67**:67–72.
- Gurdon JB, Hopwood N. 2000.** The introduction of *Xenopus laevis* into developmental biology: of empire, pregnancy testing and ribosomal genes. *International Journal of Developmental Biology* **44**:43–50.
- Harrington LA, Harrington AL, Yamaguchi N, Thom MD, Ferreras P, Windham TR, Macdonald DW. 2009.** The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression. *Ecology* **90**:1207–1216 DOI [10.1890/08-0302.1](https://doi.org/10.1890/08-0302.1).
- Herrel A, Van der Meijden A. 2014.** An analysis of the live reptile and amphibian trade in the USA compared to the global trade in endangered species. *The Herpetological Journal* **24**:103–110.
- Hersteinsson P, Macdonald DW. 1992.** Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos* **64**:505–515 DOI [10.2307/3545168](https://doi.org/10.2307/3545168).
- Holt RD. 1977.** Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* **12**:197–229 DOI [10.1016/0040-5809\(77\)90042-9](https://doi.org/10.1016/0040-5809(77)90042-9).
- Jacobs J. 1974.** Quantitative measurement of food selection. *Oecologia* **14**:413–417 DOI [10.1007/BF00384581](https://doi.org/10.1007/BF00384581).
- Kazadi M, Bruyn LD, Hulselmans J. 1986.** Ecological notes on the stomach contents of *Xenopus laevis* (Daudin, 1803) (Amphibia: Anura) collected in Ruanda. *Annales de la Societe Royale Zoologique de Belgique* **116**:227–234.
- Knickle DC, Rose GA. 2014.** Dietary niche partitioning in sympatric gadid species in coastal Newfoundland: evidence from stomachs and CN isotopes. *Environmental Biology of Fishes* **97**:343–355 DOI [10.1007/s10641-013-0156-0](https://doi.org/10.1007/s10641-013-0156-0).
- Kobel HR, Pasquier LD, Tinsley RC. 1981.** Natural hybridization and gene introgression between *Xenopus gilli* and *Xenopus laevis laevis* (Anura: Pipidae). *Journal of Zoology* **194**:317–322 DOI [10.1111/j.1469-7998.1981.tb04584.x](https://doi.org/10.1111/j.1469-7998.1981.tb04584.x).
- Kumschick S, Vimercati G, De Villiers FA, Mokhatla M, Davies SJ, Thorp CJ, Rebelo A, Measey GJ. 2017.** Impact assessment with different scoring tools: how well do alien amphibian assessments match? *Neobiota* **33**:53–66 DOI [10.3897/neobiota.33.10376](https://doi.org/10.3897/neobiota.33.10376).

- Leibold MA, McPeck MA. 2006.** Coexistence of the niche and neutral perspectives in community ecology. *Ecology* **87**:1399–1410
[DOI 10.1890/0012-9658\(2006\)87\[1399:COTNAN\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1399:COTNAN]2.0.CO;2).
- Leivas PT, Leivas FW, Moura MO. 2012.** Diet and trophic niche of *Lithobates catesbeianus* (Amphibia: Anura). *Zoologia (Curitiba)* **29(5)**:405–412
[DOI 10.1590/S1984-46702012000500003](https://doi.org/10.1590/S1984-46702012000500003).
- Lillo F, Faraone FP, Valvo ML. 2010.** Can the introduction of *Xenopus laevis* affect native amphibian populations? Reduction of reproductive occurrence in presence of the invasive species. *Biological Invasions* **13**:1533–1541 [DOI 10.1007/s10530-010-9911-8](https://doi.org/10.1007/s10530-010-9911-8).
- Lobos G, Measey GJ. 2002.** Invasive populations of *Xenopus laevis* (Daudin) in Chile. *Herpetological Journal* **12**:163–168.
- MacArthur RH, Levins R. 1967.** The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* **101**:377–385 [DOI 10.1086/282505](https://doi.org/10.1086/282505).
- MacArthur RH, Pianka ER. 1966.** On optimal use of a patchy environment. *American Naturalist* **100**:603–609 [DOI 10.1086/282454](https://doi.org/10.1086/282454).
- McCoid MJ, Fritts TH. 1989.** Growth and fatbody cycles in feral populations of the African clawed frog, *Xenopus laevis* (Pipidae), in California with comments on reproduction. *The Southwestern Naturalist* **34**:499–505 [DOI 10.2307/3671508](https://doi.org/10.2307/3671508).
- Measey GJ. 1998a.** Terrestrial prey capture in *Xenopus laevis*. *Copeia* **1998(3)**:787–791
[DOI 10.2307/1447816](https://doi.org/10.2307/1447816).
- Measey GJ. 1998b.** Diet of feral *Xenopus laevis* (Daudin) in South Wales, UK. *Journal of Zoology* **246**:287–298 [DOI 10.1111/j.1469-7998.1998.tb00159.x](https://doi.org/10.1111/j.1469-7998.1998.tb00159.x).
- Measey GJ. 2001.** Growth and ageing of feral *Xenopus laevis* (Daudin) in South Wales, UK. *Journal of Zoology* **254**:547–555 [DOI 10.1017/S0952836901001054](https://doi.org/10.1017/S0952836901001054).
- Measey GJ. 2011.** *Ensuring a future for South Africa's frogs: a strategy for conservation research*. Pretoria: South African National Biodiversity Institute.
- Measey J. 2016.** Overland movement in African clawed frogs (*Xenopus laevis*): a systematic review. *PeerJ* **4**:e2474 [DOI 10.7717/peerj.2474](https://doi.org/10.7717/peerj.2474).
- Measey GJ, De Villiers AL. 2014.** *Xenopus laevis* (Daudin, 1802) Diet. *African Herp News* **61**:16–18.
- Measey GJ, Rödder D, Green SL, Kobayashi R, Lillo F, Lobos G, Rebelo R, Thirion JM. 2012.** Ongoing invasions of the African clawed frog, *Xenopus laevis*: a global review. *Biological Invasions* **14(11)**:2255–2270 [DOI 10.1007/s10530-012-0227-8](https://doi.org/10.1007/s10530-012-0227-8).
- Measey GJ, Vimercati G, De Villiers FA, Mokhatla MM, Davies SJ, Edwards S, Altwegg R. 2015.** Frog eat frog: exploring variables influencing anurophagy. *PeerJ* **3**:e1204
[DOI 10.7717/peerj.1204](https://doi.org/10.7717/peerj.1204).
- Measey GJ, Vimercati G, De Villiers FA, Mokhatla M, Davies SJ, Thorp CJ, Rebelo AD, Kumschick S. 2016.** A global assessment of alien amphibian impacts in a formal framework. *Diversity and Distributions* **22**:970–981 [DOI 10.1111/ddi.12462](https://doi.org/10.1111/ddi.12462).
- Measey J.** Where do African clawed frogs come from? An analysis of trade in live *Xenopus laevis* imported into the USA. *Salamandra*. In Press.

- Measey J, Davies S, Vimercati G, Rebelo A, Schmidt W, Turner AA. 2017.** Invasive amphibians in southern Africa: a review of invasion pathways. *Applied Biodiversity Conservation-Bothalia* 47(2):a2117 DOI 10.4102/abc.v47i2.2117.
- Morris EK, Caruso T, Buscot F, Fischer M, Hancock C, Maier TS, Meiners T, Müller C, Obermaier E, Prati D, Socher SA. 2014.** Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. *Ecology and Evolution* 4(18):3514–3524 DOI 10.1002/ece3.1155.
- Neu CW, Byers CR, Peek JM. 1974.** A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 38(3):541–545 DOI 10.2307/3800887.
- O'Reilly JC, Deban SM, Nishikawa KC. 2002.** Derived life history characteristics constrain the evolution of aquatic feeding behavior in adult amphibians. In: Aerts P, D'Aout K, Herrel A, Van Damme R, eds. *Topics in functional and ecological vertebrate morphology*. Aachen: Shaker Publishing, 153–190.
- Palomares F, Caro TM. 1999.** Interspecific killing among mammalian carnivores. *The American Naturalist* 153:492–508 DOI 10.1086/303189.
- Patto CE. 1998.** A simple stomach flushing method for small frogs. *Herpetological Review* 29:156–156.
- Pianka RR. 1973.** The structure of lizard communities. *Annual Review of Ecology and Systematics* 4:53–74 DOI 10.1146/annurev.es.04.110173.000413.
- Picker MD. 1985.** Hybridization and habitat selection in *Xenopus gilli* and *Xenopus laevis* in the south-western Cape Province. *Copeia* 1985:574–580.
- Picker MD, De Villiers AL. 1989.** The distribution and conservation status of *Xenopus gilli* (Anura: Pipidae). *Biological Conservation* 49:169–183 DOI 10.1016/0006-3207(89)90034-7.
- R Core Team. 2015.** R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available at <https://www.R-project.org/>.
- Rebelo R, Amaral P, Bernardes M, et al. 2010.** *Xenopus laevis* (Daudin, 1802), a new exotic amphibian in Portugal. *Biological Invasions* 12:3383–3387 DOI 10.1007/s10530-010-9757-0.
- Rehage JS, Barnett BK, Sih A. 2005.** Behavioral responses to a novel predator and competitor of invasive mosquitofish and their non-invasive relatives (*Gambusia* sp.). *Behavioral Ecology and Sociobiology* 57:256–266 DOI 10.1007/s00265-004-0850-1.
- Ridewood W. 1897.** On the structure and development of the hyobranchial skeleton and larynx in *Xenopus* and *Pipa*; with remarks on the affinities of the Aglossa. *Journal of the Linnean Society of London Zoology* 26:53–128 DOI 10.1111/j.1096-3642.1897.tb00243.x.
- Schoonbee H, Prinsloo J, Nxiweni J. 1992.** Observations on the feeding habits of larvae, juvenile and adult stages of the African clawed frog, *Xenopus laevis*, in impoundments in Transkei. *Water SA* 18:227–227.
- Schriever TA, Williams DD. 2013.** Ontogenetic and individual diet variation in amphibian larvae across an environmental gradient. *Freshwater Biology* 58:223–236 DOI 10.1111/fwb.12044.

- Simmonds MP. 1985.** Interactions between *Xenopus* species in the southwestern Cape Province, South-Africa. *South African Journal of Science* **81**:200.
- Simpson EH. 1949.** Measurement of diversity. *Nature* **163**:688 DOI [10.1038/163688a0](https://doi.org/10.1038/163688a0).
- Sokol OM. 1969.** Feeding in the pipid frog *Hymenochirus boettgeri* (Tornier). *Herpetologica* **25**:9–24.
- Solé M, Beckmann O, Pelz B, Kwet A, Engels W. 2005.** Stomach-flushing for diet analysis in anurans: an improved protocol evaluated in a case study in Araucaria forests, southern Brazil. *Studies on Neotropical Fauna and Environment* **40**:23–28 DOI [10.1080/01650520400025704](https://doi.org/10.1080/01650520400025704).
- Thiemann GW, Iverson SJ, Stirling I, Obbard ME. 2011.** Individual patterns of prey selection and dietary specialization in an Arctic marine carnivore. *Oikos* **120**:1469–1478 DOI [10.1111/j.1600-0706.2011.19277.x](https://doi.org/10.1111/j.1600-0706.2011.19277.x).
- Van Sittert L, Measey GJ. 2016.** Historical perspectives on global exports and research of African clawed frogs (*Xenopus laevis*). *Transactions of the Royal Society of South Africa* **71**:157–166 DOI [10.1080/0035919X.2016.1158747](https://doi.org/10.1080/0035919X.2016.1158747).