Seasonal variation in abundance and diversity of eavesdropping frog-biting midges (Diptera, Corethrellidae) in a neotropical rainforest

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Abstract. 1. In the tropics, precipitation patterns result in seasonal fluctuations in the abundance and distribution of plant and animal species. Tropical predators and parasites are therefore faced with seasonal changes in prey and host availability.

2. This study investigates the seasonal interaction among a specialised ectoparasite, eavesdropping frog-biting midges (*Corethrella* spp.), and their anuran hosts, examining how the abundance and diversity of the frog-biting midge community fluctuate between the rainy (host abundant) and dry (host sparse) seasons.

3. Midges were captured in both the rainy and dry seasons using acoustic playbacks of calls from a common frog species that breeds during the rainy season, the túngara frog (*Engystomops, Physalaemus, pustulosus*). During the dry season túngara frog choruses are absent. To explore seasonal shifts in host preference or changes in the midge community due to host specificity, midges were also captured using playbacks of calls from a frog that breeds during the dry season, the pug-nosed tree frog (*Smilisca sila*).

4. While the overall abundance of midges decreased in the dry season, only slight differences in the relative abundance between midge species were found. These results suggest that midge populations can shift between hosts as they become available across seasons, allowing adult populations of frog-biting midges to persist year-round. To overcome the challenge of detecting and localising different host species, it is proposed that frog-biting midges have evolved a generalised acoustic template, allowing them to respond to a broad range of available hosts, regardless of seasonal host composition.

Key words. *Corethrella*, *Engystomops pustulosus*, frog-biting midges, phenology, *Smilisca sila*, tropical seasonality.

Introduction

Seasonal variation in community structure is a widespread phenomenon (Forrest & Miller-Rushing, 2010). The life-history strategies of many plants and animals depend on specific environmental conditions and resource availability that fluctuate with seasonality in abiotic factors. While seasonal variation in community composition is readily recognised in temperate ecosystems, tropical communities are sometimes assumed to be relatively uniform throughout the year (Wolda, 1988; Kishimoto-Yamada & Itioka, 2015). Precipitation regimes in tropical areas, however, result in pronounced seasonality with accentuated rainy and dry periods (Portig, 1965) that determine local ecological processes. Breeding, for instance, in some animal species, such as insects and amphibians, is directly reliant on rainfall patterns (Toft, 1980; Wolda, 1988). Leaf, flower, and seed production in tropical plants can also vary widely with precipitation (Reich, 1995). Seasonal cycles further extend to predators and parasites, who are affected by seasonal variations in abundance of their prey and hosts (Altizer *et al.*, 2006; Thompson *et al.*, 2012; Kishimoto-Yamada & Itioka, 2015). In general, in the tropics, differences among species in their responses to precipitation

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results in seasonal variation in the abundance and distribution of species.

Phenological patterns in tropical plants and animals have been widely explored (Plants: Reich, 1995; Insects: Wolda, 1978; Anurans: Cynthia *et al.*, 2005; Mammals: O'Connell, 1989; Birds: Karr, 1976). Less is known, however, about seasonal changes in predator–prey and parasite–host interactions. For predators and parasites, such predictable changes in the abundance and distribution of prey and host species may result in changes in behaviour such as diet shifts (Ben-David *et al.*, 1997; Beck *et al.*, 2007), migration to follow migrating prey (Madsen & Shine, 1996), dormancy (Turbill *et al.*, 2011), or diapause, where development at a specific stage is arrested until conditions are more favourable (Denlinger, 1986). This challenge is expected to be accentuated for parasites given their more intimate, specialised relationship with their victims and their greater need to track host availability (Raffel *et al.*, 2008). In this study, we examine the phenology of a guild of specialised ectoparasite, frog-biting midges (*Corethrella* spp.) in a community with marked differences in host composition between seasons.

Frog-biting midges of the genus *Corethrella* (Family: Corethrellidae) parasitise anurans, obtaining blood meals to support reproduction (McKeever, 1977). Unlike most haematophagous insects, female midges rely on sound to find their hosts, eavesdropping on the advertisement calls of male frogs and toads (McKeever & Hartberg, 1980; Bernal *et al.*, 2006). Tropical anurans do not call year-round, however, and their breeding period often tracks seasonal patterns in precipitation (Duellman & Trueb, 1994). This challenge of shifting host availability for the midges is further complicated by their short life cycle, lasting about a month (Mckeever & French, 1991; Borkent, 2008), which results in different generations experiencing different seasons, and thus different potential available hosts. Given that frog-biting midges depend on anuran-emitted mating calls to locate their host, and on the blood meals they acquired for egg production, particular strategies to survive and reproduce despite pronounced seasonal variation in anuran calling activity are expected. We propose two hypotheses to explain how frog-biting midges could tolerate such drastic seasonality in host availability. On one hand, behavioural adaptations such as shifts in diet between generations could compensate for seasonal changes in host abundance. Differences in the acoustic properties of the mating calls of different anuran species, however, would require broad auditory filters which would allow the midges to detect and localise calls with diverse features. Alternatively, frog-biting midges could lay dormant during the season when their main host is not breeding. Frog-biting midges could, for example, be active and breed mostly during the rainy season when anurans are abundant. In turn, some species of frog-biting midges could be specialised to feed from the few species of anurans breeding during the dry season. This type of seasonal partitioning would result in different communities of frog-biting midge in different seasons.

To obtain a more complete understanding of how seasonality in host abundance affects frog-biting midges, we investigated the abundance and diversity of this guild during the rainy and dry seasons in a tropical community. During the rainy season, April to November, in the forests of Panama, frog-biting
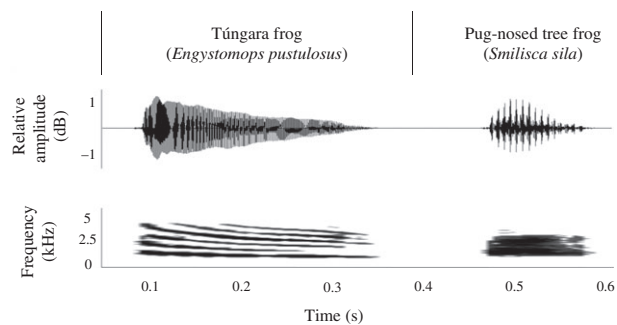

Fig. 1. Oscillogram (top) and sonogram (bottom) of túngara frog and pug-nosed tree frog advertisement calls. For the túngara frog call, an example of a simple 'whine' call is shown. Túngara frog whine sweeps from an average dominant frequency of 900 to 400 Hz over the course of 400 ms (Ryan, 1985). Although túngara frogs can produce a complex multi-note call consisting of a 'whine' and 'chucks' (Ryan, 1985), only playbacks of simple calls were used in this study. Pug-nosed tree frogs have only one note type, a noisy 'squawk' of variable duration, between 20 and 150 ms, and with an average dominant frequency of 2500 Hz (Tuttle & Ryan, 1982).

midges are attracted in high numbers to the mating call of the most common anuran species in this area, the túngara frog (*Engystomops pustulosus*) (Bernal *et al.*, 2006). Túngara frog choruses, however, are almost completely absent in the dry season (December to April). During the dry season, when precipitation is low, the less abundant pug-nosed tree frog (*Smilisca sila*) calls and breeds (Heyer, 1976). Pug-nosed tree frog choruses are not formed during the rainy season, and no other anuran species in this area consistently calls during the dry season. The calls of túngara frogs and pug-nosed tree frogs differ greatly in their acoustic structure and complexity (Fig. 1), imposing a potential challenge for the midges to detect and recognise their host. Here we investigate how abundance and diversity of frog-biting midges attracted to túngara frog calls change as their host's abundance changes across seasons. To identify seasonal host shifts or changes in the midge community due to host specificity, we compare the abundance and diversity of midges attracted to pug-nosed tree frog calls with those of midges attracted to túngara frogs calls within the same season.

Materials and methods

Study site

We conducted acoustic playbacks at eight locations in the forest around Gamboa, Republic of Panama (9°07.0′N, 79°41.9′W), within 0.5 km of a water source with breeding frogs. To ensure independence between collections, the locations were separated by at least 1 km. Gamboa receives an average of 2148 mm year^{-1} of rainfall and precipitation rates define two seasons, rainy and dry. At the height of the rainy season, October, Gamboa receives an average of 306 mm in a month. Comparatively, at the height of the dry season, February and March, Gamboa receives <20 mm of rainfall (Niedzialek

& Ogden, 2012). Gamboa is situated along both the Chagres River and the Panama Canal.

Acoustic stimuli

To create the recordings used for acoustic playbacks, we selected 10 individual calls each from a collection of túngara and pug-nosed tree frog chorus recordings with low background noise. Each call used was produced by a different male to capture potential interindividual differences. Recordings were created using only single-note, simple calls from each species. For túngara frogs, only the initial note in a call, the 'whine' (see Fig. 1), was used to remove any confounding effect of call complexity. A single playback recording consisted of one 'simple', non-complex call, from a single individual frog broadcast at a rate of one call every 2 s, at an amplitude of 82 dB SPL re. 20 μPa at 1 m from the speaker. This call rate and peak amplitude represent the average value for calls produced by male túngara frogs in this population (Ryan, 1985). To compare the abundance and species of frog-biting midges attracted to túngara frog and pug-nosed tree frogs, we also used this call rate and amplitude for pug-nosed tree frog playbacks. While the natural call rate and amplitude of pug-nosed tree frog calls deviate from the values we used, our goal was to investigate the effect of call structure on frog–midge attraction during the rainy and dry season. Each night, a random playback recording was chosen from the set of 10 to broadcast.

Collecting methods and identification

Eavesdropping midges were collected for a 45-min period, 2 h following sunset, using modified CDC mosquito traps (McKeever & Hartberg, 1980) placed over Pignose portable amplifiers (Model 7–100; Pignose-Gorilla, North Las Vegas, Nevada). These sound traps were placed at ground level, the natural calling elevation of both túngara frogs (surface of small ephemeral ponds) and pug-nosed tree frogs (beside waterfalls and along the banks of fast-flowing streams). Only one location was sampled per night, and each location was sampled three times over the duration of the season for a total of 24 nights. We collected insects using playbacks of túngara frog calls during the rainy season, from 22 June to 1 August 2014, and using both túngara and pug-nosed tree frog calls during the dry season from 8 January to 28 February 2015. Túngara and pug-nosed tree frog calls were always played at separate locations from one another to ensure independence between the samples. Although there is evidence that some species of frog-biting midges may be facultatively autogenous, and are thus able to lay their first batch of eggs without a blood meal, using frog call sound traps is the only reliable method to capture adult female midges. Other cues commonly used by other haematophagous insects, such as CO_2, can actually deter frog-biting midges (Bernal & de Silva, 2015). We thus relied on sound traps under the assumption that the proportion of individuals not using frog calls in the population at a given time does not change between seasons. Following the collection period, all collected insects were euthanised in the freezer and counted the next day before being preserved in 75% ethanol for species identification.

For each of the three sets of collected midges, we randomly selected a subset of the specimens for identification. Each subset represented 25% of the collected specimens originally collected at each set. We identified 2329 specimens for túngara frog calls in the rainy season, 999 specimens for túngara frog calls in the dry season, and 319 specimens for pug-nosed tree frog calls in the dry season. Midges were identified using an established key for *Corethrella* in the Neotropics (Borkent, 2008; Amaral & Pinho, 2015). Midges were dissected following Borkent (2008) and mounted into Euparal (Cranston & Krosch, 2011). Voucher material is stored in the entomological collection of Purdue University.

Statistical methods

All statistical analyses were conducted using the 'vegan' package (Oksanen *et al.*, 2017) in R v. 3.3.0 (R Development Core Team, 2016). Captured midges were compared across seasons, rainy and dry, and between frog species, túngara and pug-nosed tree frogs. We compared differences in overall midge abundance using independent samples *t*-tests. We compared diversity using Shannon indices, $H = -\sum_{i=1}^{S} p_i \log_b p_i$, where p_i is the proportion of species i, S is the number of species, and b is the base of the logarithm (Hill, 1973), and Pielou's evenness, $J = H' / \log(S)$, where H' is the Shannon index calculated using natural logarithms (Hill, 1973). We constructed log-transformed ranked abundance distribution curves using pre-emption, log-normal, Zipf, and Zipf–Mandelbrot models. To account for rare species we used Beal's smoothing to estimate the probability of occurrence of each species for each treatment (De Cáceres & Legendre, 2008). Different ordination methods could not be applied due to the small size and homogeneity of the frog-biting midge community.

Results

Frog-biting midge communities between seasons

Sound traps broadcasting túngara frog calls were successful at attracting frog-biting midges both during the rainy and dry season (Table 1). During the rainy season, a total of 9052 corethrellids from eight species were captured using sound traps playing túngara frog calls. Significantly fewer midges were captured using túngara frog calls in the dry season, a total of 3936 comprising six species (*t*-test, $t = 3.37$, $P = 0.001$; Table 2a). Both seasons were dominated by a single species, *Corethrella ranapungens* Borkent, which represented over 85% of the specimens identified in our samples. While the subdominant species differed between seasons [*Corethrella edwardsi* Lane (Lane, 1942) and *Corethrella carariensis* Borkent for the rainy and dry seasons, respectively], the difference between the subdominant species and the other less common species was slight in comparison. Only one species, *C. carariensis*, was more abundant in the dry season (48 collected) than in the rainy season (20 collected).

Table 1. Number of frog-biting midges (*Corethrella* spp.) collected and identified in different seasons. Midges were collected using túngara frog and pug-nosed tree frog calls in the rainy season, and using both túngara frog and pug-nosed tree frog calls in the dry season. Approximately 25% of the specimens from each collected set were identified. The percentages represent the proportion of individuals identified from each sample.

Acoustic playback	Season	Total number collected	Number identified	C. appendiculata	C. aurita	C. belkini	C. blanda/pallida	C. carariensis	C. edwardsi	C. ranapungens	C. quadrivittata
Túngara frog calls (*Engystomops pustulosus*)	Rainy	9052	2329 (25.73%)	11 (0.47%)	75 (3.22%)	3 (0.13%)	58 (2.49%)	20 (0.86%)	84 (3.61%)	2010 (86.30%)	68 (2.92%)
Túngara frog calls (*E. pustulosus*)	Dry	3936	999 (25.38%)	0	32 (3.20%)	0	10 (1.00%)	48 (4.80%)	11 (1.10%)	893 (89.39%)	5 (0.50%)
Pug-nosed tree frog calls (*Smilisca sila*)	Dry	1253	319 (25.46%)	0	52 (16.30%)	1 (0.31%)	3 (0.94%)	14 (4.39%)	1 (0.31%)	247 (77.43%)	1 (0.31%)

Both Shannon diversity and Pielou's evenness for frog-biting midges were slightly higher in the rainy season than in the dry season (Table 2b). The slopes of the ranked abundance curves, fitted using Zipf models (Table 2c), for the rainy and dry seasons were similar (Fig. 2a,b), suggesting that the relative abundances of the midge community are similar between seasons. Although there were two species absent from the dry season that were identified in the rainy season, *Corethrella appendiculata* Grabham (Grabham, 1906) and *Corethrella belkini* Borkent, these species were rare. Use of Beal's smoothing to take into consideration the midges attracted to túngara frog calls in both seasons revealed a high probability that both *C. appendiculata* (66.08%) and *C. belkini* (76.78%) occur in the dry season and are attracted to túngara frog calls.

Frog-biting midge communities feeding on different anuran species

During the dry season, significantly fewer midges were attracted to pug-nosed tree frog calls (1253 individuals from seven species) than to túngara frog calls (3936 individuals from six species) (*t*-test, $t = 5.19$, $P < 0.00001$; Table 2a). Like túngara frog calls, *C. ranapungens* was the dominant species, representing 77.43% of the specimens we identified attracted to the calls of the pug-nosed tree frog. The difference between the less common species was more pronounced, with the subdominant species in the sample, *Corethrella aurita* Borkent, representing 16.30% of the total sample. *Corethrella aurita* was also the only species attracted in greater numbers to pug-nosed tree frog calls than to túngara frog calls during the dry season, representing only 3.20% of the individuals sampled attracted to túngara frog call.

As a result of the slightly lower dominance of *C. ranapungens*, Shannon diversity and Pielou's evenness were higher for midges attracted to pug-nosed tree frog calls than for those attracted to túngara frog calls (Table 2b). Furthermore, three midge species in the dry season attracted to pug-nosed tree frog calls were represented by only one individual. The slope of the ranked abundance curve, fitted using a Zipf–Mandelbrot model (Table 2c), was steeper than for the dry season túngara frog sample; however, this steepness is probably the result of the three species with only one individual (Fig. 2c). The steep initial slope between the first three most abundant species suggests a more uniform distribution in comparison to the midges attracted to túngara frog calls. As with túngara frog calls in the dry season, *C. appendiculata* was not detected in the midges attracted to pug-nosed tree frogs. Similarly, using Beal's smoothing to take the rainy season datasets into consideration indicates that there is a high probability that *C. appendiculata* (67.35%) occurs in the dry season and is also attracted to pug-nosed tree frog calls.

Discussion

Our results reveal significant seasonal differences in overall frog-biting midge abundance. This variation in abundance coincides with changes in host availability, increasing during the rainy season when many species of anurans breed, and

Table 2. Comparative statistics and calculations for each of the three sets of frog-biting midges (*Corethrella* spp.). (a) Significance of the difference in abundance between midges collected in the rainy and dry seasons using túngara frog calls, and the difference between midges collected using túngara frog calls and pug-nosed tree frog calls in the dry season. (b) Diversity and evenness calculations for each set. (c) The Akaike information criterion (AIC) values of all fitted rank abundance curve models.

		Túngara frog – rainy	Túngara frog – dry	Pug-nosed tree frog – dry
(a)	Overall abundance (*P*-value)	0.001	<0.0001	
(b)	Shannon diversity	0.627	0.479	0.729
	Pielou's evenness	0.302	0.267	0.375
(c)	Ranked abundance curve models (AIC)			
	Pre-emption	835.23	193.65	35.24
	Log-normal	454.32	123.90	36.00
	Zipf	**302.84**	**69.39**	39.40
	Zipf–Mandelbrot	304.84	71.39	**34.36**

Bolded values indicate lowest AIC value.

decreasing during the dry season when only one species breeds. Precipitation rates may also directly affect frog-biting midge abundance given that standing water is required for egg and larvae development (Borkent, 2008). Most midge species, however, use permanent waterbodies for reproduction, such as lake margins, lagoons, and ponds (Borkent, 2008). High abundance of these types of waterbodies in our study area, such as the Charges River and the Panama Canal, suggests that host abundance, not breeding site availability, is the limiting resource for most midge species during the dry season. Consistent with this idea, the only midge species present during the rainy season that was absent in the dry season, *C. appendiculata*, breeds in water-filled tree holes that are created when rainwater collects in tree cavities but which then dry out during the dry season (Yanoviak, 1999). Although we did not capture *C. appendiculata* during the dry season, it is likely that this species was still present in this system, but at extremely low densities, and was not detected due to its rarity. Even during the rainy season, when midge abundance was at its peak, *C. appendiculata* made up only 0.47% of the midge community. In general, the seasonal fluctuation we found in frog-biting midges is similar to the seasonal patterns of other tropical insects in areas with distinctive rainy and dry seasons. Such fluctuations in abundance, for example, have been described for tropical coleopterans (Wolda, 1992), hemipterans (Wolda, 1989), homopterans (Wolda, 1978), hymenopterans (Slaa, 2006), lepidopterans (Devries & Walla, 2001; Grøtan *et al.*, 2012), and neuropterans (Michel & Cadet, 2009). In these examples, the insect species also lack periods of dormancy, and abundance typically peaks during the rainy season, synchronising with seasonal variations in host or food availability (Wolda, 1988; Kishimoto-Yamada & Itioka, 2015).

There are other behaviour mechanisms, in addition to dormancy, that frog-biting midges might use to account for low host availability in the dry season. Female midges could shift to taking blood meals from different hosts, specifically pug-nose tree frogs that, unlike most tropical anuran species, breed exclusively in the dry season. Host species breadth has previously been demonstrated within the rainy season. Midge species captured in this study have been captured using playbacks of calls from a variety of anuran species that breed during the rainy

season (gladiator frogs, *Hyla rosenbergi*; yellow tree frogs, *Dendropsophus microcephalus*; leaf litter toads, *Bufo typhonius*; and red-snouted tree frogs, *Scinax ruber*; Borkent, 2008). In this study, we found that host breadth extends across seasons as well, and frog-biting midges are attracted to pug-nosed tree frog calls during the dry season.

Other eavesdroppers that depend on anuran calls (e.g. frog-eating bats, *Trachops cirrhosus*) also shift their diet across seasons to account for changes in prey abundance. When food resources are scare, bats can expand the breadth of their diet to utilise novel, but available, prey (Jones *et al.*, 2014). Challenges of seasonality are different between bats and midges, however, considering the difference in life span relative to season length. The life of a bat spans multiple rainy and dry seasons, and the challenges of seasonal changes in prey availability must be solved at an individual level. Comparatively, the life cycle of a frog-biting midge is only about 1 month (Mckeever & French, 1991; Borkent, 2008), and multiple generations occur during a season. Again, the challenge to shifting hosts is that the mating calls of different anuran species vary greatly in acoustic structure and complexity. The behaviour of frog-biting midges suggests they have evolved broad auditory filters allowing them to respond to a broad range of acoustic cues. Three lines of evidence, in particular, support the presence of generalised acoustic templates in at least some species of frog-biting midges. First, as mentioned earlier, frog-biting midges are attracted to the mating calls of multiple anuran species of frog-biting midge (Borkent, 2008). Second, the midges also respond to calls of frogs that do not occur in sympatry (barking treefrog, *Hyla gratiosa*; Borkent, 2008). Finally, frog-biting midges are attracted to playbacks of pure tones over a broad range of frequencies (100–4000 Hz; Meuche *et al.*, 2016). Such a generalised acoustic template would allow an individual midge, regardless of host species composition, to respond to all available hosts.

In the dry season, a greater number of midges were attracted to túngara frog calls than to pug-nosed tree frog calls, suggesting that midges prefer túngara frog calls, even during the season when calling túngara frogs are absent. Túngara frogs are abundant and widespread across Middle and northern South America, and male frogs produce conspicuous mating calls at high rates
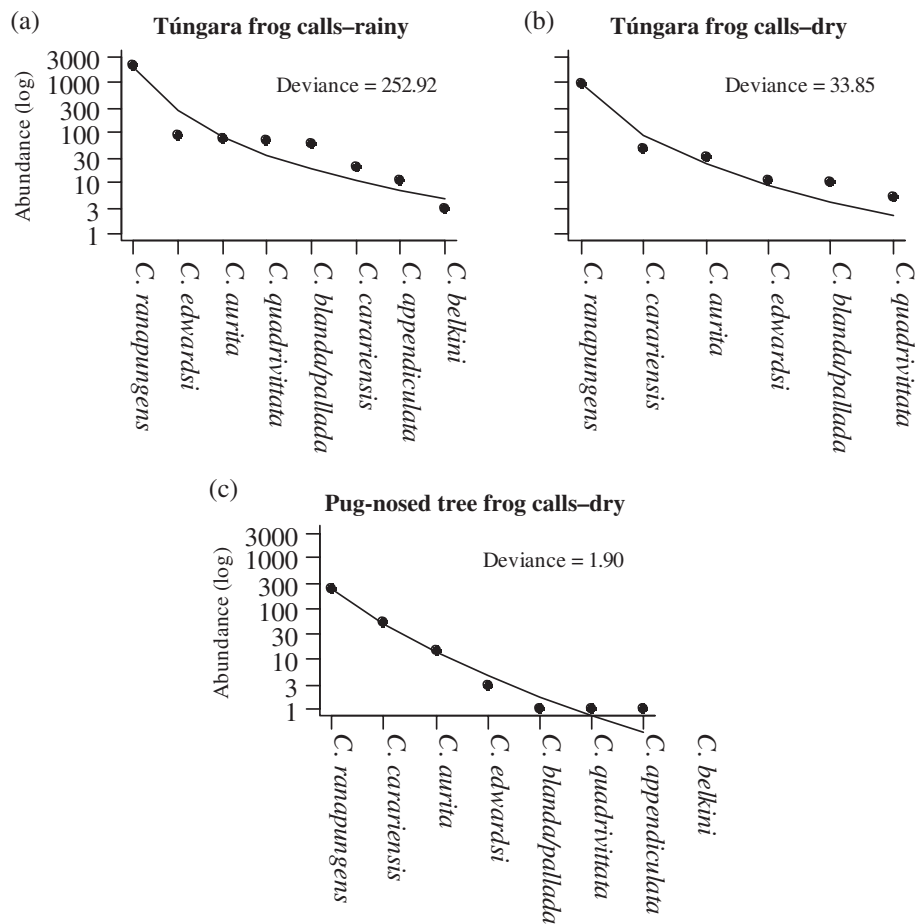
Fig. 2. Ranked abundance distribution curves for all sets of collected frog-biting midges. (a) Midges collected in the rainy season using túngara frog calls. (b) Midges collected in the dry season using túngara frog calls. (c) Midges collected in the dry season using pug-nosed tree frog calls. Curves were fitted using Zipf, Zipf, and Zipf–Mandlebrot models respectively, based on lowest Akaike information criterion values.

during the breeding season, attracting many acoustic eavesdroppers (Page *et al.*, 2014). The tuning curves of the auditory systems for all frog-biting midge species are unknown, and it is not even clear how they are hearing anuran calls (Bernal *et al.*, 2006). The fact, however, that the species captured in this study prefer túngara frogs even when these frogs are less abundant suggests that the species in this system are more sensitive to túngara frog calls than to the calls of the less common pug-nosed tree frog. This could be due to specialisation of the auditory system, or it could be a result of general auditory bias. For example, túngara frog calls are, on average, longer in duration than pug-nosed tree frog calls, making them more conspicuous. The exception to the trend, however, *C. aurita*, was more abundant in the dry season and was attracted in greater numbers to pug-nosed tree frog calls, suggesting that this species, at least, may be an auditory and seasonal specialist. The other seasonal exception, *C. carariensis*, was also more abundant in the dry season, but was equally attracted to both túngara calls and pug-nose tree frog calls, suggesting that some other factor besides host specialisation is driving higher *C. carariensis* dry season abundance.

Further studies exploring the natural history and behaviour of these two midge species are necessary.

In all the samples collected, *C. ranapungens* was clearly the dominant species, comprising 86% of identified specimens. However, the degree of year-to-year variation in the relative abundance between species is unclear. A midge collection from the same area conducted a decade earlier during the rainy season found that *C. edwardsi* was the most common species, comprising an average of 73% of the samples collected using túngara frog calls (Bernal *et al.*, 2006). In comparison, *C. edwardsi* comprised only 3.6% of our samples during the rainy season. In other groups of tropical insects, patterns in year-to-year abundance are highly variable, with some species fluctuating wildly while others remain largely stable (Wolda, 1978), so changes in the relative abundance of frog-biting midge species across years would not be unexpected. To gain a more accurate view of the relative abundance of frog-biting midges in this system, a more prolonged study spanning multiple years would be valuable. Regardless, our results indicate distinct seasonality in the abundance of frog-biting midge species within a single year, a pattern that is expected to be consistent between

years given that, even with yearly fluctuations, seasonal trends in abundance within a year are often maintained (Wolda, 1978; Kishimoto-Yamada & Itioka, 2015).

On a final note, frog-biting midges can transfer diseases between hosts, and feeding from multiple host species can have implications regarding disease transmission within the anuran community (McKeever & French, 2000). In particular, frog-biting midges feeding on túngara frogs at our study site can transmit a blood parasite, trypanosomes (*Trypanosoma tungarae*; Bernal & Pinto, 2016), that could be transmitted to other species of anurans. As midges shift to taking blood meals from pug-nosed tree frogs during the dry season, trypanosomes may be transmitted between calling male anurans of different species. Multiple hosts could allow trypanosomes to persist between seasons as well, with male pug-nosed tree frogs serving as primary host during the dry season. Trypanosomes add another layer of complexity to the seasonal interaction between anurans and midges, providing an opportunity to investigate disease transmission dynamics in the light of vector and host seasonality. Further research in this area is needed, however, as the ecology, life cycle, and pathological effects of trypanosomes in this system are still unknown.

In this study, we demonstrated pronounced seasonality in a group of specialised ectoparasites, frog-biting midges, corresponding with changes in host availability. We also found little change in the relative abundance of midge species between seasons, and a lack of evidence of dormancy in the midge species in this system. Our results indicate that, as host availability changes between rainy and dry seasons, midges shift to an alternative host, the pug-nosed tree frog. We propose that frog-biting midges have evolved broad auditory filters, allowing midges in different generations to overcome the challenge of detecting and recognising the mating calls of different hosts. This facilitates a more generalist strategy regarding host selection, allowing frog-biting midges to persist year-round. Understanding these host–parasite interactions in the context of seasonality is critical to understanding how tropical communities change over time. This information is particularly important now, considering that precipitation patterns are changing, rainfall events are becoming more extreme, and the contrast between seasons is decreasing as a result of warming sea surface temperatures linked to anthropogenic climate change (Aguilar *et al.*, 2005; Chang *et al.*, 2015).

Acknowledgements

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