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Abstract

Insect migrations represent large movements of resources across a landscape, which are attractive to predators capable of detecting and catching them. Brazilian free-tailed bats (*Tadarida brasiliensis* I. Geoffroy, 1824) consume migratory noctuid moths, which concentrate in favourable winds resulting in aggregations of prey that attract bats hundreds of metres above ground. While *T. brasiliensis* are known to feed on these aggregations of migratory moths, changes in their foraging behaviours have not been linked to moth migration events. We investigated possible shifts in the bats' foraging behaviours when moths are migrating with respect to altitude and moth abundance. We recorded 1,104 *T. brasiliensis*' echolocation call passes at ground level and at altitudes of ~100m and ~200m above ground level. We found proportionally more bat activity at higher altitudes when migratory moth abundance was high. We also found that bats decreased call frequency and bandwidth and increased call duration at higher altitudes, and behaved similarly with increasing moth abundance even at ground level. Our results support predictions that bats change foraging behaviour in response to seasonal availability of migratory moths, and document alterations in echolocation call parameters that are consistent with optimizing prey detection.

Keywords Echolocation, Migration, Altitude, Predator-prey interaction, Moths, Brazilian free-tailed bats

Draft

Introduction

Animal migrations can result in large and rapid shifts in the distribution of biomass across landscapes. Although often overlooked, insect migrations hundreds of meters above ground involve more biomass, and may have greater impact on ecosystem function, than any other migratory system (Drake and Gatehouse 1995). For example, an estimated 3200 tons of insect biomass flows over southern England annually (Hu et al. 2016). Migratory moths typically increase fat reserves before migration and provide an attractive resource for insectivorous animals (Angelo and Slansky 1984). However, because moth migrations often occur at altitudes hundreds of meters above ground level (AGL) (Drake and Gatehouse 1995) and vary greatly in time and trajectory (Showers et al. 1989; Showers et al. 1993) their availability is ephemeral and can be difficult to predict.

To exploit migratory prey resources, a predator must detect migration events and adjust foraging behaviours to find and capture prey (Cortes-Avizanda et al. 2011). Bats are known to eat migratory insects including major crop pests (Kronwitter 1988; Lee and McCracken 2005; Leelapaibul et al. 2005). In North America, Brazilian free-tailed bats (*Tadarida brasiliensis* I. Geoffroy, 1824) and migratory noctuid moths – including major crop pests that these bats eat in abundance – have received considerable attention (Wolf et al. 1990; Lee and McCracken 2005; McCracken et al. 2008; Reichard et al. 2009; McCracken et al. 2012; Krauel et al. 2015), and provide an excellent system for examining interactions between highly mobile predators and migratory prey.

In late summer and early autumn in Texas, high air temperatures, lack of rainfall, and scarcity of host crops (Meyer and Brown 1985; Vermeire et al. 2009) result in reduced

availability of local insect prey (McNaughton et al. 1989) for the large numbers of *T. brasiliensis* that inhabit the region. At the same time, female bats are at their lowest fat reserve levels, after having weaned their pups (Pagels 1975; O'Shea 1976), and are challenged with regaining fat to fuel their own autumn migration to more southern latitudes (Krauel et al. 2015). Waves of lipid-rich, southward-bound migrating moths take advantage of favourable northerly winds following cold fronts (Rankin and Burchsted 1992; Pair et al. 1987; Westbrook 2008) and provide essential resources for these bats at this time (McCracken et al. 2012; Krauel et al. 2015, 2017).

Tadarida brasiliensis fly and forage at high altitudes (Williams et al. 1973; Griffin and Thompson 1982), with echolocation call feeding buzzes recorded at 847 m AGL (McCracken et al. 2008; Gillam et al. 2009). These high altitude flights have been attributed to pursuit of migratory insect prey, and McCracken et al. (2008) documented a peak in bat activity at between 400-500 m AGL, the same altitudes as the strong prevailing winds that are used by migratory insects to facilitate long distance movement (Westbrook 2008). Fecal DNA analysis reveals spikes in bats' consumption of *Helicoverpa zea* Boddie, 1850 (corn earworm moths) coincident with these moths' spring and autumn migrations (McCracken et al. 2012), and consumption of these and other migratory moth species coincident with their autumn migrations (Krauel et al. 2017). Increased bat foraging activity at altitudes used by migrating moths, and increased consumption of moths during periods of moth migration, indicate that bats take advantage of these migrations. However, previous work has not examined high-altitude feeding behaviours of bats in response to migratory insect availability.

If bats increase their foraging efforts where and when moths are migrating, bats might also adjust their echolocation behaviour accordingly. The echolocation calls of *T. brasiliensis* are highly variable (Simmons et al. 1978; Gillam and McCracken 2007) and plastic (Ratcliffe et al. 2004; Gillam et al. 2010). Gillam et al. (2009) demonstrated that at higher altitudes *T. brasiliensis* employed calls that were lower in frequency and bandwidth and longer in duration than were the calls used near ground level. Use of lower frequencies reduces the atmospheric attenuation, thereby improving detection distance (Lawrence and Simmons 1982), while increasing call duration and decreasing bandwidth should also increase the chances of bats' detecting prey-generated echoes (Neuweiler 1990). Thus, the call parameter adjustments observed in relation to altitude by Gillam et al. (2009) may reflect bats foraging for widely dispersed prey in open space.

Our objective was to investigate foraging behaviours of *T. brasiliensis* in response to altitude and the movements of migratory moths in autumn. We hypothesized that bats would adjust where they forage and also their echolocation behaviour in response to moth migration patterns. Specifically, we predicted (1) that foraging activity would increase at higher altitudes during periods of increased abundance of migrating moths, and (2) that search phase echolocation call parameters would differ with altitude and with prey density.

Materials and methods

Study system

We collected data between 25 August and 13 November 2012, near Frio Cave, Uvalde County, Texas (TX), and in surrounding agricultural areas. Frio Cave (29° 26' 4.488" N,

-99° 41' 5.028" W) is approximately 120 km west of San Antonio, TX, on private ranch land on the southern edge of the Edwards Plateau, and, with 1-2 million bats, is one of the largest known cave colonies of *T. brasiliensis* (Betke et al. 2008). The area south of the cave consists of ranch land and farmland known as the Winter Garden. Primary summer crops include corn, cotton, soybean and sorghum; in the fall, some fields contain corn or late cotton crops, while others are used for vegetables or are left fallow. High numbers of noctuid moths are found throughout the study area during late spring and summer when host crops are available. However, most of the local population of the most abundant moth species, *H. zea*, enters pupal diapause by mid-September (Lopez and Hartstack 1985).

Noctuid moths migrate with assistance of favourable winds (Chapman et al. 2008a; Chapman et al. 2008b), and moth migration in autumn is initiated by cold front passage through areas where adult moths are sensitive to relevant cues such as changes in day length and air temperature, and possibly wind direction (Muller and Tucker 1986). Prevailing winds in the study area are typically from the south, and thus southward movement in autumn is likely to be restricted to periods of northerly winds associated with passing cold fronts (Sparks et al. 1986; Showers et al. 1993). In the North American Great Plains region, cold fronts often move southward from Midwestern states into Texas, but may dissipate at ground level before passing all the way through the study area. However, high velocity northerly winds may continue at higher altitudes despite a lack of local frontal passage, and may carry migrating insects (J. Westbrook, pers. obs.). In the study we report here, we identified passage of large-scale cold fronts over the

study area by visual analysis of frontal patterns on Daily Surface Weather charts (NOAA 2012) following Lee et al. (2012).

Migratory moth activity

Direct measurement of nocturnal insect abundance aloft is difficult due to relatively low aerial concentrations of insects at high altitudes within a dark environment (Westbrook 2008). We used two methods, pheromone trapping and bat fecal sampling, as proxy estimates for migratory moth abundance during sampling periods. Earlier studies have shown that both of these proxies of migratory moth abundance are positively correlated with cold front passage (Krauel et al. 2015, 2017), as anticipated if cold front passage is a key factor determining migratory moth movements in autumn (Krauel et al. 2015).

We collected moths daily during the study period from pheromone traps deployed at three replicate agricultural sites and one site located on a nearby livestock ranch approximately 4 km from crops, which were likely to have been attractive to moth pests (Fig 1a). Trapping sites ranged southeast along an 8 km transect from the cave. Each site contained 5 pheromone traps, each trap baited with pheromone lures to attract adult male moths of different noctuid pest species: *H. zea*, *Agrotis ipsilon* Hufnagel, 1766 (black cutworm), *Spodoptera frugiperda* J. E. Smith, 1797 (fall armyworm), *Trichoplusia ni* Hübner, 1803 (cabbage looper), and *Pseudaletia unipuncta* Haworth, 1809 (true armyworm). Each site also included a blacklight trap (BioQuip, Model 2851L: 22W) to monitor local insects. We replaced pheromone lures within recommended expiration

periods, usually weekly, and checked all insect traps daily. All collected moths were frozen for later analysis.

We used an analysis of insect DNA extracted from bat fecal samples (Krauel et al. 2017) as a second estimate of migratory moth activity in the study area. We caught *T. brasiliensis* as they returned to the cave before dawn approximately every other day (Krauel et al. 2015), and conducted sample collection and molecular diet analysis as described by Krauel et al. (2017). Dates of bat fecal sampling did not always exactly match nights when bat activity was measured, but were not more than one night apart. We used the `na.spline` function of R package “`zoo`” (Zeileis and Grothendieck 2005) to interpolate the number of migratory moth species present in bat diet on adjacent activity sampling nights.

Foraging activity at ground-level and aloft

We tested bat response to moth migration events by recording bat echolocation calls at ground-level and aloft during and after passage of cold fronts on nights with northerly winds. All acoustic recordings were made using SM2Bat detectors (Wildlife Acoustics Inc., Concord, MA, USA) at the moth-trapping site located 11 km SW of Frio Cave (29° 20' 3.552" N, -99° 42' 47.6274" W; Fig. 1a). We acquired ground-level recordings at 1.5 m AGL, and deployed two additional detectors at higher altitudes at the same site using a 3.3-m³ Skyhook Helikite (Fig. 1b, Allsopp Helikites Ltd., Hampshire, UK; Verhoeven et al. 2009). The Helikite is a helium-filled hybrid kite-balloon that enables lift in low winds and remains stable in winds to ca. 15 m s⁻¹. We attached higher-altitude detectors

to spars taped to 300 kg test Dyneema line and deployed the Helikite using an electric winch (Goodwinch Ltd., Devon, UK).

We let out at least 350 m of line in the late afternoon, well before bats began flying in the area, with the detectors attached below the Helikite to fly at altitudes of ~100 m and ~200 m above ground level (AGL). The SM2Bat detectors deployed aloft were modified by removing the external casing and switching to low-mass power supply. We packaged the bat detectors in Styrofoam cylinders that were tapered so that the cylinders vaned into the wind with the microphones protected leeward of the tapered end of the cylinder (Fig. 1c, McCracken et al. 2008). We activated detectors at the time of initial deployment and deactivated them as they were removed from the Helikite line at the end of each flight. We configured the ground-based and air-borne detectors identically, and set them to begin recording when ultrasonic signals were detected and to continue recording for 10 s, or as long signals were present. Approximate height of detectors at start of recording sessions was calculated using a Bushnell Sport 450 Laser Rangefinder (Bushnell Corporation, Overland Park, KS, USA). Altitude estimates were generally conservative as the Helikite tended to rise slightly during recording sessions as wind increased after sunset.

Echolocation Call Analysis

We used Kaleidoscope software (v 0.1.8, Wildlife Acoustics Inc., Concord, MA, USA) to extract echolocation call files from compressed recordings, where each file included a series of echolocation calls representing a pass by one or more bats (Sherwin et al. 2000). We used Sonobat software (v 3.1.4 West, Sonobat, Arcata, CA, USA), which

provides quantitative quality assessments of bat calls in addition to probability of species identification, to identify files containing high quality calls (80% quality or higher), to identify calls to bat species where possible, and to generate call parameter data on the highest quality calls in each call file. We included files confirmed by Sonobat as containing only calls of *T. brasiliensis*. Some call files represented passes by multiple individuals, particularly during periods of high insect activity. Because it was not possible to accurately determine the number of bats contributing to each sequence, we conservatively considered each call file to represent a single bat pass (Sherwin et al. 2000). We defined feeding as the presence of one or more “feeding buzz” call sequences (Hayes 2000) in a pass, as identified by listening to time-expanded recordings. Calls that appeared to represent social interactions or had incomplete “feeding buzz” sequences were not included in the analysis of feeding activity.

To evaluate differences in echolocation call parameters attributable to altitude and moth explanatory variables, we retained only call files containing high-quality search phase calls ($\geq 80\%$ quality level, as assessed by Sonobat) that were unambiguously identified by both software and human eye as belonging to *T. brasiliensis*. Files with interference (e.g., insect calls) also were excluded from further analysis, as they invoked a jump in the high-pass filter from 5 kHz to 25 kHz which also may have inadvertently filtered out the often < 25 kHz echolocation calls of *T. brasiliensis*. For analysis, we used the following Sonobat call parameters: duration (ms), frequency (frequency of the maximum amplitude of the call, kHz), bandwidth (difference between highest and lowest frequency, kHz), and inter-call interval (time between current and previous call, ms). We defined a sequence of search phase calls as those with >50 ms between calls (Griffin et

al. 1960); calls with <50 ms between them were excluded from further analysis. We measured a single, focal call from each sequence of calls so as not to average across calls from what could have been different individuals. Focal calls were those with the highest amplitude without evidence of saturation (“clipping”) in a given call sequence. To reduce the probability of sampling the same bat twice, we allowed at least one second of silence to elapse in the .wav file before identifying and measuring the next call. We evaluated parameters from high-quality single search phase calls from 358 bat passes at the upper Helikite detector, 462 bat passes at the lower Helikite detector, and 1035 bat passes at ground level.

Statistical analysis

We compared bat behaviour between ground level and aloft using an activity index which represented the mean number of *T. brasiliensis*’ search phase call .wav files recorded aloft divided by the number of call files recorded at ground level. We modeled feeding buzzes similarly, using a buzz index representing the mean number of all feeding buzzes recorded aloft divided by those at ground level. Because there were two detectors aloft and only one at ground level, we estimated activity and feeding aloft using the mean value for the detectors at 100 m and 200 m AGL. While recording time varied between nights, these indices provide relative measures that are insensitive to different sample sizes. We evaluated relative foraging activity and feeding buzzes by calculating the Pearson’s product-moment correlation between activity index or buzz index and the numbers of migratory moth species in bat diets and total numbers of moths caught in pheromone traps on the flight night as explanatory variables. We investigated the

relationship between *T. brasiliensis*' echolocation call design, moth abundance, and altitude by creating full factorial fit models (linear regression with interaction terms) with each call parameter as the response variable and altitude (ground, 100 m AGL, and 200 m AGL) and the number of migrants in bat diet as explanatory variables. We assessed the relative contributions of individual variables in regression models using the R^2 partitioned by averaging over orders, as calculated by the `calc.relimp` function in the `relaimpo` package (Grömping 2016). We performed all statistical analyses in R (R 2016).

Results

We conducted recording sessions during 13 nights between 29 August and 19 October 2012. Mean recording duration was 2.64 h, after sunset and between 2100-0000 h. These recordings documented bat activity in relation to cold fronts passing over the study area on 7, 13, 18, and 29 September, and 5 and 17 October. Detector altitudes varied with wind conditions, but were 100 ± 22 m (mid-altitude Helikite detector) and 200 ± 36 m (higher-altitude Helikite detector) AGL. We recorded a total of 1,784 bat passes, of which 1,104 were confirmed by Sonobat software as belonging to *T. brasiliensis*. In addition, we recorded calls identified as having been emitted by *Eptesicus fuscus* Palisot de Beauvois, 1796, *Eumops perotis* Schinz, 1821, *Lasiurus blossevillii* Lesson and Garnot, 1826, *Lasiurus cinereus* Palisot de Beauvois, 1796, *Lasionycteris noctivagans* Le Conte, 1831, *Perimyotis subflavus* F. Cuvier, 1832, and *Myotis* spp. (likely to be mostly *M. velifer* J. A. Allen, 1890, given our study location). Calls from *L. noctivagans* and *P. subflavus* were recorded only on the detector deployed at ground level. The remaining bat passes could not be confidently attributed to a single species or contained calls from multiple species.

Echolocation call activity of *T. brasiliensis* was always higher at ground level than aloft, but there was relatively more activity aloft than at ground level, measured as the activity index, as the number of migratory moth species in bat diet increased (Table 1, $r=0.79$, $t=3.93$, $df=9$, $p=0.0035$). Feeding buzz activity also was higher at ground level than aloft, but was not related to either measure of migratory moth abundance (Table 1). Moth captures in pheromone traps did not significantly explain variation in activity with altitude ($p=0.86$).

Call duration increased with altitude: calls were longer in duration at 200 m AGL compared to those at 100 m AGL, which were, in turn, longer than those produced by *T. brasiliensis* at ground level (Figure 2a, Adj $R^2=0.20$, $F_{5,1849}=94.6$, $p<0.0001$). Peak frequency and call bandwidth also varied with altitude: bats at ground level used calls with significantly higher peak frequency (Figure 2b, Adj $R^2=0.20$, $F_{5,1849}=95.8$, $p<0.0001$) and greater bandwidth (Figure 2c, Adj $R^2=0.14$, $F_{5,1849}=59.6$, $p<0.0001$) than did bats at either altitude aloft. Altitude was the most important factor in explaining variation in call duration and frequency (Table 2), accounting for 15 and 16%, respectively, but only 4% of variation in bandwidth. Moth abundance explained 8% of variation in bandwidth, but only 4-5% of variation in duration and frequency.

Specifically, call duration increased with moth abundance, while call bandwidth and call peak frequency both decreased (Table 2), following the same pattern seen in the changes in call variables with increasing altitude. Interestingly, the significant interactions between altitude and moth abundance for call bandwidth and call peak frequency (and the nearly significant interaction for call duration) are mainly due to bats flying at ground level (see the relatively steep slope for frequency and bandwidth at

ground level vs. aloft as moth abundance increases, Figure 2b and 2c). That is, under conditions of higher moth abundance, *T. brasiliensis* at ground level apparently adjusted their echolocation behaviour such that it was more similar to that observed from bats at altitude. Across all altitudes and moth abundances, we found significant support for the well-established positive relationship (Simmons et al. 1978) between call duration and call interval ($R^2=0.04$, $F_{5,1614}=71.14$, $p < 0.0001$) and equally well-established negative relationships (Simmons et al. 1978) between call interval and call peak frequency ($R^2=0.18$, $F_{5,1614}=358.8$, $p < 0.0001$) and bandwidth ($R^2=0.20$, $F_{5,1614}=412.7$, $p < 0.0001$).

Discussion

We provide support for predator behavioural response to prey fluctuations due to seasonal insect migration, as well as behavioural context for previously observed patterns of bat activity aloft. By linking changes in foraging behaviour at high altitude with consumption of migratory moths, our results offer support for *T. brasiliensis* using moth migration in autumn as a key resource to rebuild their own pre-migratory fat reserves (Krauel et al. 2015, 2017). To our knowledge, ours is the first study to link behavioural responses of bats to insect migration events.

Earlier studies showed that *T. brasiliensis* responds to prey resource fluctuations in time and space at ground level (Davidai et al. 2015). However, *T. brasiliensis* are known to forage well above ground level (Griffin and Thompson 1982; McCracken et al. 2008) but their behaviour in response to prey at high altitudes (see Gillam et al. 2009) is unknown. While insect migration events involve vast amounts of biomass (Hu et al. 2016), these insects are spread out over time and large volumes of airspace, with maximum aerial concentrations measured at typically 10^3 to 10^4 insects per 10^6 m³

(Pedgley 1990; Beerwinkle et al. 1994). Direct sampling of insects aloft is difficult, expensive, and inefficient (Westbrook 2008). The observed correlation between increased presence of high-flying migratory moths in bats' diet and increased bat foraging activity aloft suggests that the bats' diet (Krauel et al. 2017) might serve as a reliable proxy for bat prey abundance aloft, enabling further studies of these high-altitude predator-prey interactions, but future research is needed to validate this relationship.

Gillam et al. (2009) showed that *T. brasiliensis* modify echolocation call parameters, using search phase calls with longer duration and lower frequency and bandwidth when flying at increasing altitudes. Our study confirms that earlier work and further places these call modifications within behavioural context. *Tadarida brasiliensis* have a very flexible echolocation repertoire (Simmons et al. 1979; Gillam and McCracken 2007) and calls with shorter duration and greater bandwidth may allow them to detect smaller prey as well as avoid collisions in situations where they encounter other bats or clutter near ground level (Ratcliffe et al. 2004; Gillam and McCracken 2007). Long-duration, narrow-band calls typically recorded from *T. brasiliensis* are effective for long-range detection of relatively large insect prey such as moths in large, uncluttered volumes of open air (Denzinger and Schnitzler 2013). At higher altitudes and away from background clutter, *T. brasiliensis* may benefit from using these longer duration, lower frequency call designs to receive information over greater distances (Neuweiler 1900; Schnitzler and Kalko 2000; Gillam et al. 2009).

We also document changes in echolocation call parameters relative to differences in prey levels. *Tadarida brasiliensis* use calls of greater duration, lower peak frequency, and narrower bandwidth at higher altitudes, but we show that this species makes similar

adjustments to call design as moth abundance increases, an observation that appears to be especially robust at ground level. If bats respond to increasing prey density by assuming closer proximity to the nearest prey, we would expect the opposite result (shorter calls with higher frequency and bandwidth). However, in the observed behaviour, increasing call duration will increase the overall amount of energy in the signal, increasing detection range. Further, decreasing peak frequency and bandwidth will reduce the effects of atmospheric attenuation (Lawrence and Simmons 1982), further improving detection range. More than this, by limiting call bandwidth, the amount of neural activity that will be elicited at frequency-matched neurons will also increase, improving detection range still further (Neuweiler 1990; Schnitzler and Kalko 2001). Thus, lower peak frequency and narrower bandwidth come at the cost of poorer target resolution and may limit the size of insects detected. While these results appear to contradict expected behaviour, the migratory moths targeted by the bats in this study represent high-value prey (Angelo and Slansky 1984), are larger than most other insects found in blacklight traps during the study (J. Krauel, pers obs), and are preferred by the congener bat *T. teniotis* Rafinesque, 1814 (Mata et al. 2016). Thus, these changes in echolocation behaviour may suit times of high migratory moth abundance, regardless of altitude, and suggest a possible mechanism of prey selection.

Migratory moths are often tracked using pheromone traps (McCracken et al. 2012; Davidai et al. 2015), but we did not find a relationship between bat activity aloft and pheromone trap captures. Earlier research in the study area suggested that noctuid moth captures in ground-level pheromone traps can closely match radar-documented mass movement of moths, especially in autumn (Beerwinkle et al. 1995), and pheromone trap

captures in this study tracked the passage of cold fronts which drive moth migration in the region (Sparks et al. 1986; Krauel et al. 2015). However, we found little relationship between the number of moths captured in ground-based pheromone traps and what the bats were eating (Krauel et al. 2017). This is illustrated by the night of 14 September, one day after a cold front passed through the study area. Local pheromone trap captures were low (Table 1) and thus do not suggest a concurrent migration event. However, we recorded high bat activity aloft, and high numbers of migratory moth species were identified in fecal samples from bats at Frio Cave on 12 and 15 September (Table 3; Krauel et al. 2017) also indicating migratory insect movement into the area. While increased bat activity may have been a response to local insect emergence, a blacklight trap co-located at the Helikite field site did not indicate a local emergence of large numbers of any insects. Thus, blacklight and pheromone traps appear not to have adequately reflected the insect community that was available to the bats.

Tadarida brasiliensis fly up to a range of ≥ 50 km each night while foraging (Wilkins 1989; Krauel et al. 2015). Our nightly samples pooled the diet of 15 bats, thus representing a sampling of insects over a much larger area than covered by ground-based traps, which cover hundreds of meters at most. In addition, pheromone trap data from northern locations, which might have served as sources of migratory moths, showed very high captures in early- to mid-September (Fleischer et al. 2007; Pestwatch 2016). Our samples may not accurately represent overall prey availability as they include an inherent bias due to the filter of bat detection and selection of prey (see discussion in Krauel et al. 2017). However, the apparent preference of *T. brasiliensis* for large moths (Lee and McCracken 2002, 2005) indicates this bias could enhance the odds of sampling migratory

moths. These results support our earlier finding that bat dietary analysis may measure a different prey community than local ground-level pheromone traps (Krauel et al. 2017), thus offering an alternative basis for tracking high-altitude movements of migratory moths.

Seasonal, nocturnal migrations of insects have been widely documented (Drake and Gatehouse 1995), and despite the magnitude of these resource fluctuations across the landscape (Hu et al. 2016), these nocturnal movements are often overlooked (Diehl 2013). Here, we have shown that predators such as *T. brasiliensis* do not overlook these high altitude concentrations of resources. Indeed, these predators themselves comprise a huge biomass moving high across the night sky. We expect this high-altitude phenomenon to be more widespread than this particular study system. Airborne interactions between predators and their migratory prey are poorly documented, yet almost certainly represent important, underappreciated components of an ecosystem which faces challenges due to loss of habitat and climate change (Parmesan 2001).

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Ethical Standards

All experiments complied with the current laws of the country in which they were performed. The authors declare that they have no conflict of interest.

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Table 1 Foraging activity of Brazilian free-tailed bats (*Tadarida brasiliensis*) represented as total number of call files recorded at ground level, 100 m, and 200 m above ground level in Uvalde Co, Texas, USA, 2012, with two indicators of migratory moth prey abundance.

Recording	# Moth	# Moths	<u>Total bat passes</u>			<u>Feeding Buzzes</u>		
Date	spp in diet	in traps	Ground	100 m	200 m	Ground	100 m	200 m
29-Aug	5.58	2	70	8	7	4	0	0
30-Aug	5.75	4	22	25	2	1	1	1
8-Sep	8.00	46	4	--	2	0	--	0
9-Sep	7.69	18	17	4	9	4	0	0
14-Sep	10.31	37	57	101	66	16	15	7
18-Sep	9.04	21	10	8	21	1	0	2
29-Sep	5.42	162	73	25	30	2	3	5
30-Sep	5.00	58	40	9	12	5	2	0
1-Oct	3.97	81	174	60	46	9	3	1
6-Oct	6.00	438	18	16	7	1	3	0
7-Oct	7.91	313	64	45	27	8	1	0
18-Oct	11.00	44	--	7	14	--	2	0
19-Oct	12.04	36	--	2	2	--	0	0

Note: Migratory moth abundance is estimated using the number of migratory moth species found in bats’ diet and the total catch (4 crop pest species) at all pheromone traps, on each sampling day. See text for details. Samples with no data were due to equipment malfunction.

Table 2. Relative importance of variables in echolocation call parameter models

Parameter	Altitude	Moths	Interaction
Duration	0.156	0.045	0.002
Frequency	0.146	0.050	0.009
Bandwidth	0.039	0.079	0.020

Note: Values are the R^2 contribution averaged over orderings among altitude, number of migratory moth species in bats' diet, and their interaction in linear regression with key echolocation call parameters call duration, frequency of maximum energy, and bandwidth. For example, altitude (ground, 100 m, or 200 m) explained 15.6% of all variation in call duration.

Table 3. Migratory moth species consumed by *T. brasiliensis* on nights surrounding 14 September 2012.

12 September	Both nights	15 September
<i>Nomophila nearctica</i> Munroe, 1973	<i>Agrotis malefida</i> Guenée, 1852	<i>Spodoptera exigua</i> Hübner, 1808
<i>*Spodoptera frugiperda</i>	<i>Leucania insueta</i> Guenée, 1852	<i>*Helicoverpa zea</i>
<i>Anticarsia gemmatalis</i> Hübner, 1818	<i>Euchromius ocella</i> Haworth, 1811	<i>*Trichoplusia ni</i>
	<i>Bulia deducta</i> Morrison, 1875	<i>Condica sutor</i> Guenée, 1852
	<i>Hypena scabra</i> Fabricius, 1798	<i>Tathorhynchus exsiccata</i> Lederer, 1855
	<i>Peridroma saucia</i> Hübner, 1808	
	<i>Plutella xylostella</i> L., 1758	

Note: Asterisks indicate species included in pheromone trapping.

Fig 1 Map of study area and diagram of equipment. Map (a) inset shows location of Frio Cave (open circle) and pheromone trap deployment sites north of Uvalde, Uvalde County, TX. Helikite (b) used to raise detectors aloft. Inset shows detector in purpose-made Styrofoam casing designed to stabilize detector and minimize noise from wind. See text for further details.

Fig 2 Effect of altitude and moth count on echolocation call parameters. Observed changes in (a) call duration (ms), (b) frequency of maximum energy (kHz), and (c) bandwidth (kHz) in *T. brasiliensis*’ search phase calls at ground level and at approximately 100 m and 200 m above ground level. Lines represent change in call parameter values at each altitude with increasing moth abundance; shaded areas indicate 95% confidence intervals on linear regression. The horizontal axis represents the number of migratory moth species found in bat diet on the night the call was recorded. Call duration increased, and frequency and bandwidth decreased at higher altitudes, and a similar effect was found especially at ground level as moths increased.

Duration (ms)

Frequency (kHz)

Bandwidth (kHz)

Number of Migratory Moth Species in Diet

--- Ground - - - 100 m — 200 m