Weather-driven dynamics in a dual-migrant system: moths and bats

13 **Jennifer J. Krauel**[1]*, **John K. Westbrook**[2] and **Gary F. McCracken**[1]

[1]*University of Tennessee, Knoxville, TN 37996, USA; and* [2]*U.S. Department of Agriculture, Agricultural Research* **1** *Service, College Station, TX, USA*

Summary

1. Animal migrations generate large spatial and temporal fluctuations in biomass that provide a resource base for many predator–prey interactions. These interactions are often driven by continent-scale weather patterns and are difficult to study. Few studies have included migratory animals on more than a single trophic level or for periods spanning multiple entire seasons.

2. We tracked migrations of three species of agricultural pest noctuid moths over the 2010–2012 autumn seasons as the moths travelled past a large colony of migratory Brazilian free-tailed bats (*Tadarida brasiliensis*) in Texas.

3. Increases in moth abundance, mass of bats and duration of bat activity outside of the cave were correlated with passage of cold fronts over the study area and related increases in northerly wind. Moth responses to weather patterns varied among species and seasons, but overall moth abundances were low in late summer and spiked after one or more cold front passages in September and October.

4. Changes in bat mass and behaviour appear to be consequences of bat migration, as cave use transitioned from summer maternity roost to autumn migratory stopover sites.

5. Weather-driven migration is at considerable risk from climate change, and bat and moth responses to that change may have marked impacts on agricultural systems and bat ecosystem services.

Key-words: Chiroptera: Molossidae, community-level impacts, ecosystem services, generalist predators, *Helicoverpa zea*, Lepidoptera: Noctuidae, *Spodoptera frugiperda*, synoptic weather, *Trichoplusia ni*

Introduction

Animal migrations represent huge pulses of resources across landscape-scale areas (Chapman *et al.* 2012; Bauer & Hoye 2014; Dingle 2014), and the scope and magnitude of migrations are expected to markedly impact ecosystem dynamics (Yang *et al.* 2008). Because most migrants are fuelled by fat reserves (Bairlein 2002; Newton 2008; Hein, Hou & Gillooly 2012), migrant prey should be a valuable resource for predators. However, migration events are often weather driven (Shamoun-Baranes, Bouten & van Loon 2010) and thus difficult for predators to predict. Game theory suggests that non-aggressive generalist predators should be best able to take advantage of unpredictable resources (Overington, Dubois & Lefebvre 2008),

that is social predators are able to work together to locate the resources in space and time, and generalists can modify their behaviours to respond to a variety of prey. Migration-related patterns of movement and response across large spatial scales are important to understand, yet are rarely studied from an integrative perspective such as predator–prey interaction (Bowlin *et al.* 2010).

High-altitude nocturnal insect migrations (Chapman, Drake & Reynolds 2011; Drake & Reynolds 2012) are an attractive resource for predators (Rankin & Burchsted 1992). Continent-spanning insect migrations have been documented in Australia, East Asia, Africa, Europe and North America (Drake & Gatehouse 1995). Some of the most destructive agricultural insect pests are migratory moths in the family Noctuidae (Hill 2008). These moths are generalists, fecund and highly mobile. Some noctuids are obligate migrants in temperate areas and use migration to avoid temperature extremes or to track suitable

*Correspondence author. E-mail: jkrauel@vols.utk.edu

host plants. Others are facultative migrants, able either to migrate when conditions are favourable, or to enter diapause, a genetically programmed period of quiescence (Triplehorn & Johnson 2005), to wait for more favourable climate conditions and host plants. Round-trip movement of migratory noctuids has been relatively well established in Europe (Chapman *et al.* 2008, 2010, 2012; Alerstam *et al.* 2011) and East Asia (Feng *et al.* 2003, 2009), including documentation of mechanisms driving migratory patterns (Chapman *et al.* 2012). Research on migratory pest movement in North America, however, has been biased towards spring when crops are most vulnerable to damage (Leskinen *et al.* 2011). While much is thus known about northward movement of noctuid moths into North America in spring (Domino *et al.* 1983; Fitt 1989; Showers *et al.* 1989; Beerwinkle *et al.* 1994; Pair *et al.* 1995), until recently, there was doubt that these insects underwent a return migration in autumn (Johnson 1987; McNeil 1987; Pair *et al.* 1987; Gould *et al.* 2002), and little is known about the mechanisms influencing this behaviour (Showers *et al.* 1993).

Many animal migrations, including migrations of insects (Drake & Farrow 1988), are influenced by climate and weather (Shamoun-Baranes, Bouten & van Loon 2010). In North America, northward migration in spring is aided by typical patterns of low pressure in the Northern Plains and high pressure off the eastern coast, resulting in northward air flow from the Gulf of Mexico into the agricultural regions of the Great Plains (Johnson 1995). This pattern is periodically reversed in autumn when barometric pressure gradients generate a series of cold fronts moving south from the Plains towards the southern USA (Johnson 1995). Cold front passage is generally followed by a few days of northerly wind with higher than normal speed (Showers *et al.* 1993).

While many predators are likely to take advantage of migratory insects after they arrive, aerial predators such as some birds and bats are able to locate and capture them en route. There is evidence that insectivorous bats share foraging information (Wilkinson 1992; Ratcliffe & ter Hofstede 2005; Gillam 2007; Dechmann *et al.* 2009), and among these, Brazilian free-tailed bats (*Tadarida brasiliensis*) are social generalist predators (Lee & McCracken 2005) that forage at high altitudes (McCracken *et al.* 2008). They roost in large colonies in the direct paths of migratory moth routes, can use unpredictable resources (Lee & McCracken 2005; McCracken *et al.* 2008, 2012) and are known to eavesdrop on conspecifics to find prey (Gillam 2007). Brazilian free-tailed bats are themselves long-distance migrants (Krauel & McCracken 2013) and must gain mass in autumn (O'Shea 1976) to fuel their own migration.

This study examines a dual-migrant system in southern Texas to investigate relationships between weather patterns, fluctuations in migratory noctuid moth abundances, and migration-related changes in behaviour and resource acquisition of Brazilian free-tailed bats. We hypothesized that changes in noctuid moth numbers in the air are linked to changes in regional (cold fronts) and local (wind) meteorological patterns and that bat flight activity and changes in body mass are linked to the same weather patterns. We predicted that (1) local abundances of noctuid moths increase with frontal passages and favourable northerly wind, (2) bats gain mass with frontal passages and (3) bats are active for shorter periods when resources are more available, as they are able to more easily meet their foraging needs.

Materials and methods

STUDY AREA

This study took place at Frio Cave, Uvalde County, Texas (29°26′4·488″N, -99°41′5·028″W), and adjacent agricultural areas (Fig. 1). This cave is approximately 120 km west of San Antonio on private ranchland on the southern edge of the Edwards Plateau and hosts one of the largest known cave colonies of Brazilian free-tailed bats, with 1–2 million bats each summer (Betke *et al.* 2008). The area south of the cave consists of ranchland and farmland known as the Winter Garden. Primary summer crops include corn, cotton, soybean and sorghum; in autumn, some fields are used for sweet corn or late cotton crops, while others are used for vegetables or are left fallow.

MOTH MONITORING

Moth samples were collected during three field seasons: between September 8 and October 21, 2010; September 7 and November 15, 2011; and August 25 through November 13, 2012. Traps were
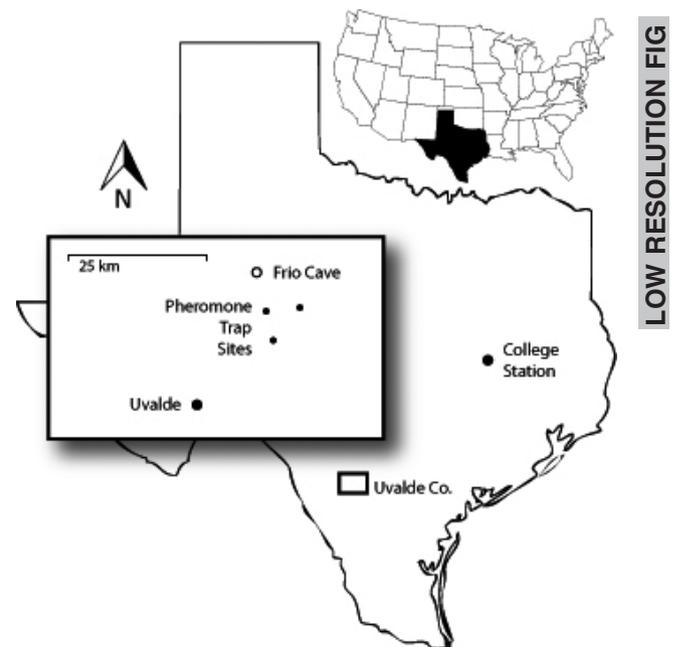

Fig. 1. Study area. Inset shows location of Frio Cave (open circle) and pheromone trap deployment sites north of Uvalde, Uvalde County, TX. Additional sites were located at College Station, TX, approximately 400 km to the northeast.

deployed at three agricultural field sites near Uvalde, Texas, ranging southeast from the cave along an 8 km transect (Fig. 1). Three additional replicates were deployed at College Station, Texas, approximately 400 km to the northeast of Frio Cave. We deployed one pheromone trap per target species spaced approximately 50 m apart at each replicate site to attract adult male moths, each baited for a specific noctuid pest: corn earworm (*Helicoverpa zea*), fall armyworm (*Spodoptera frugiperda*) and cabbage looper (*Trichoplusia ni*).

Corn earworm traps were wire cone traps baited with Trece (Adair, OK, USA) lure TR-CEW 3138; fall armyworm and cabbage looper traps were universal plastic bucket traps baited with Scentry 2 (Billings, MT, USA) component lure SC-FAW L105B and Trece lure TR-CL 3119, respectively. Lures were replaced within recommended expiration periods, usually weekly. All traps were checked daily, and moths were frozen for later analysis.

METEOROLOGICAL MONITORING

In 2010 and 2011, a VantagePro weather station (Davis Instruments, Hayward, CA, USA) near the southernmost moth field site near Uvalde recorded hourly temperature, humidity, rainfall, barometric pressure and other relevant data. Meteorological data during 2012 were acquired from the National Weather Service (NWS) weather station at the Garner Field airport, Uvalde, except for readings for barometric pressure which were acquired from the NWS weather station at the municipal airport at Hondo, Texas, approximately 61 km east of Uvalde. Wind direction data for all three seasons came from the weather station at the Garner Field airport. Patterns of northerly wind at Uvalde and at College Station were adequately correlated to assume similar temporal patterns of wind-aided autumnal migration of noctuid moths (J. Westbrook, pers. obs.).

ACOUSTIC MONITORING

We deployed Anabat II detectors (Titley Scientific, Columbia, MO, USA) approximately 25 m east and 30 m west of Frio Cave entrances to record bat activity around the cave in 2011 and 2012. Nightly foraging activity began with the main colony emergence, which was easily identified by our detectors. Acoustic signals at the cave entrances slowed after the main emergence but were continuous throughout the night. We considered the end of nightly activity time to occur when gaps of more than 10 mins separated pulses of incoming bats. Recordings of stragglers returning to the cave were discarded as not being representative of colony activity as a whole. Duration of bat flight activity was measured as the elapsed time (in hours) between start of colony emergence in the evening and end of return in the morning.

BAT DATA COLLECTION

Approximately every second day we sampled bats returning to Frio Cave after foraging, following Lee & McCracken (2002, 2005). Twenty-five bats were caught 1–2 h before dawn using padded hand nets or mist nets, individually placed in clean cloth bags, and kept in a warm, dark and quiet area. After 3 h, we recorded standardized measurements of mass, sex, reproductive status, age and forearm length and released the bats into the cave. Methods complied with approved University of Tennessee Institutional Animal Care and Use protocol no. 1947.

COLD FRONT ANALYSIS

Moth migration events in North America are likely initiated by cold front passage in areas where adult moths are sensitive to relevant cues such as changes in day length and air temperature, and possibly wind direction (Muller & Tucker 1986). In the North American Great Plains region, cold fronts often move from Kansas southward into Texas, but may dissipate at ground level before passing entirely through the study area. However, high-velocity northerly wind may continue despite the lack of a well-defined local frontal passage and may carry migrating insects (J. Westbrook, pers. obs.). Previous studies documented large numbers of insects moving southward in northerly winds directly following the leading edge of cold front passage in the Central Texas area (Beerwinkle *et al.* 1994), as noted similarly in Europe and Asia (Feng *et al.* 2003, 2009; Chapman *et al.* 2010, 2012; Chapman, Drake & Reynolds 2011). In the current study, passage of large-scale cold fronts over the study area was identified by visual analysis of frontal patterns on Daily Surface Weather charts (National Weather Service 2010–2012a) following Lee *et al.* (2012).

DATA ANALYSIS

Meteorological predictor variables were daily values for nightly amount of northerly wind, low air temperature, low dew point and low barometric pressure. Temperature, dew point and barometric pressure readings were sampled from one to three times hourly, and we used the lowest value for each variable on each day. Because moths may need northerly winds to move southward in autumn, we calculated the number of readings per night with wind from any northerly direction (<90 ° or >270 °). We considered night to include hours between local civil twilight at dusk and dawn, and wind direction was sampled three times per hour. We represented passage of cold fronts at Uvalde as a factor coded 1 for each day of frontal passage and 0 otherwise. Where moth abundances were used in analyses, we used median numbers of each moth species captured at pheromone traps across three agricultural site replicates. Moth abundance numbers, meteorological data and length of bat flight activity had statistically significant temporal autocorrelation. We removed autocorrelation and seasonal trends by taking the first difference of each daily value (DeLurgio 1998). Thus, values represent the change in each variable from the previous day.

To identify which factors best explained variation in moth abundance, we computed cross-correlations (DeLurgio 1998) between median daily numbers of moths caught in pheromone traps for each moth species and meteorological variables. Cross-correlations were considered significant when they exceeded 2 divided by the square root of the number of observations (DeLurgio 1998). Because relationships between moth numbers and predictor variables are likely to vary over time, we calculated cross-correlations for lags of up to 2 days.

We used multiple linear regression to identify factors best explaining variation in the duration of bat flight activity at the cave in 2011 and 2012. Potential factors included moth abundances and meteorological data. When duration of bat flight activity was statistically correlated with biologically meaningful lags in a variable, we included variables offset by that lag in the full regression model (Legendre & Legendre 2012). We used the stepAIC function (R package *Mass*, Venables & Ripley 2002) to

identify the best model for each year and for both years combined. Because model parameters can contribute substantially to the overall model r^2 even if they are not statistically significant in themselves, we report the relative importance for each variable in the best models (R package *relaimpo*, Grömping 2006). Relative importance describes the amount of variation in a response variable that is produced by a particular predictor variable.

To determine the relationship between changes in bat mass and cold front passages, we compiled a set of all pairs of bat mass values from consecutive sampling days over all 3 years. To increase statistical power, we constructed a boot-strapped distribution of the *t*-value of all next-sampling-day changes in bat mass by computing 5000 one-tailed paired *t*-tests on randomly selected pairs of bat mass samples. We then computed paired t-test values of changes in mass on nearest days of frontal passage and compared the *t*-value results to the overall boot-strapped distribution. As expected for this species (Wilkins 1989), female mass was consistently greater than that of males, so we analysed males and females separately. All tests were run using R (v 3.0.2, 2013-09-25, R Development Core Team 2013).

Results

We caught 35 509 moths in pheromone traps at Uvalde during the three field seasons (195 days total), 84% of which were corn earworms, and 28 145 moths in pheromone traps at College Station, Texas, of which 86·5% were corn earworms. Proportions of other species varied between years (Table S1, Supporting information). We caught 2318 Brazilian free-tailed bats during this same time, of which 64% were female and 36% male. The proportion of female to male bats did not change over any season.

Weather varied between years; 2010 was a very wet year until October (National Weather Service 2010–2012b) but had few cold front events in autumn. This was followed by extreme drought in 2011 despite much more frequent cold fronts, and that drought worsened in 2012. The amount of nightly northerly wind was positively correlated with frontal passage in all 3 years (Table S2, Supporting information). Because temperature, dew point and barometric pressure were highly correlated with cold front passage and northerly wind, for simplicity, we excluded those variables from analysis of moth abundances.

Moth abundances at pheromone traps increased the day of cold front passages in all years and sites combined. This result is likely conservative, as increased winds and lower temperatures associated with frontal passage may have made it more difficult for moths to find pheromone traps (Gregg *et al.* 1994). Responses of moths to weather varied with species, site and year (Table 1, Fig. 2a–c, see also Table S3, Fig. S1a–c, Supporting information). Overall, corn earworm numbers increased the day after frontal passage, cabbage looper numbers increased 2 days after frontal passage, and fall armyworm numbers increased the same day as frontal passage. Moths also responded to increasing northerly winds. In 2010, numbers of all moth species increased the same day that northerly wind

Table 1. Statistically significant positive cross-correlations between moth abundance and weather variables. F = passage of cold fronts, W = amount of northerly wind at night, UV = Uvalde site, CS = College Station site. Moth species: CEW (corn earworm), FAW (fall armyworm), CL (cabbage looper). Numbers represent the coefficient of correlation between median numbers of moths caught in pheromone traps and frontal passage or amount of northerly wind at the Uvalde site the same day, the day before and 2 days prior. For example, the number of corn earworm moths caught in 2010 at the College Station site was positively correlated ($r = +0.48$) with the amount of northerly wind on the same day

Moth species	Year	Site	2 days prior	Previous day	Same day
CEW	2010	CS			$W + 0.48$
	2012	CS		$F + 0.41$	$W + 0.35$
	All	CS		$F + 0.21$	$W + 0.19$
		All		$F + 0.22$	
FAW	2010	UV			$F + 0.43$
					$W + 0.47$
		CS			$W + 0.32$
	2011	UV			$F + 0.24$
		CS		$W + 0.32$	$F + 0.30$
CL	2010	UV	$F + 0.46$		
	2012	UV		$W + 0.64$	
	All	UV			$F + 0.16$
	All		$F + 0.18$		
All	All	CS			$F + 0.20$
		All			$F + 0.21$

increased, and corn earworm responded similarly in 2012. Cabbage looper numbers increased at both sites the day after northerly winds increased in 2012.

Moth numbers at College Station and Uvalde sites were temporally related (Table S4, Fig. S1a–c, Supporting information). When years are pooled, fall armyworm numbers increased a day earlier at College Station than at Uvalde, but the pattern was reversed for cabbage looper, which increased a day earlier at Uvalde than at College Station. In 2011, there was a strong correlation ($r = +0.67$) with fall armyworm numbers increasing at College Station the day before increasing at Uvalde.

Female bats gained mass over the course of the season in all 3 years (Fig. 3), and the mass gains were statistically significant in 2011 ($r^2 = 0.60$, $P < 0.001$) and 2012 ($r^2 = 0.33$, $P < 0.001$); lack of statistical significance in 2010 may be due to a shorter sampling period. Variability of female mass increased as the season progressed, based on standard deviation of mass in 2010 ($r^2 = 0.38$, $P = 0.002$), 2011 ($r^2 = 0.31$, $P < 0.001$) and 2012 ($r^2 = 0.41$, $P < 0.001$). Males also gained mass in 2011 ($r^2 = 0.61$, $P < 0.001$) and 2012 ($r^2 = 0.12$, $P = 0.03$), but not in 2010 ($r^2 = 0.004$, $P = 0.77$). Male masses were less variable than those of females, with a small but statistically significant increase in variability only in 2011 ($r^2 = 0.17$, $P = 0.02$). Both male and female bat mass increased more in association with cold front passages than on other consecutive sampling days (males: mean
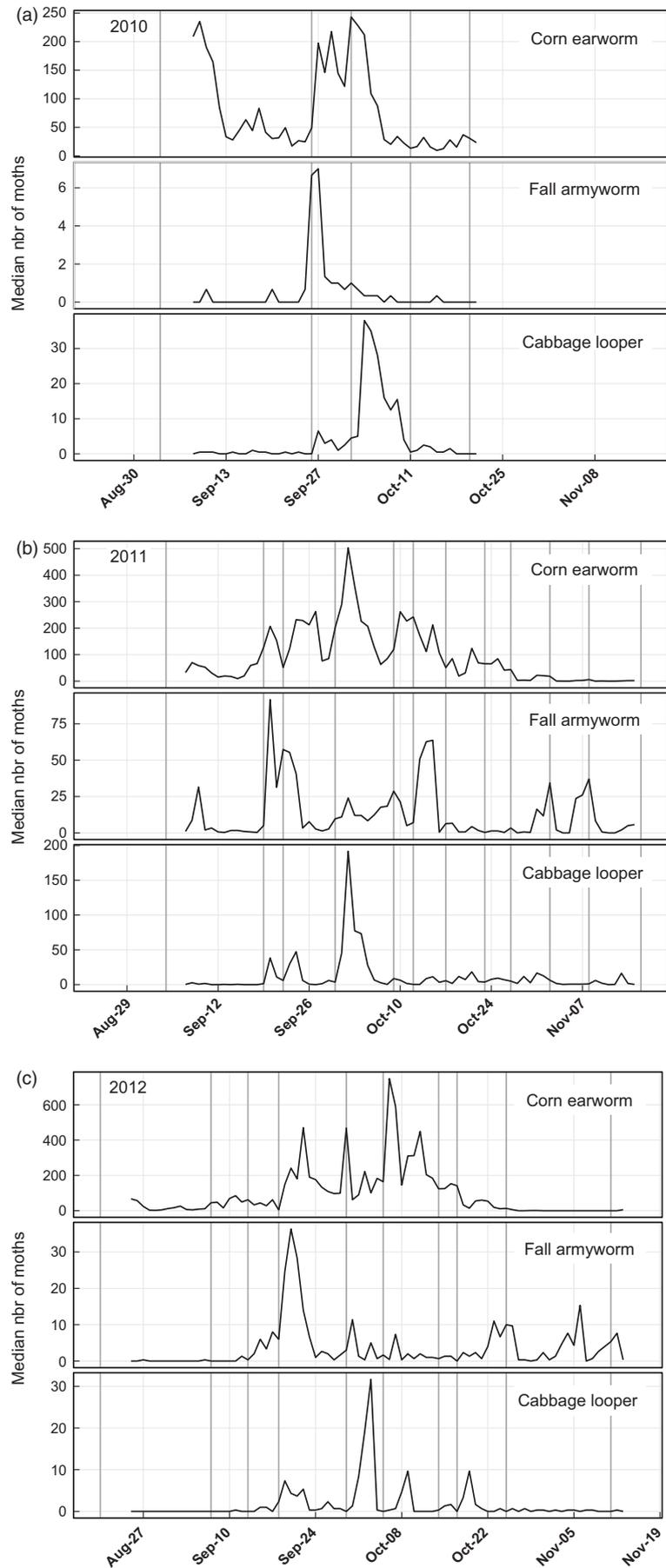
Fig. 2. (a–c) Median moth captures by species at pheromone traps in (a) 2010, (b) 2011 and (c) 2012. Note that the scale of the vertical axes varies between species and years. Vertical grey lines represent day of cold front passage at Uvalde, TX.
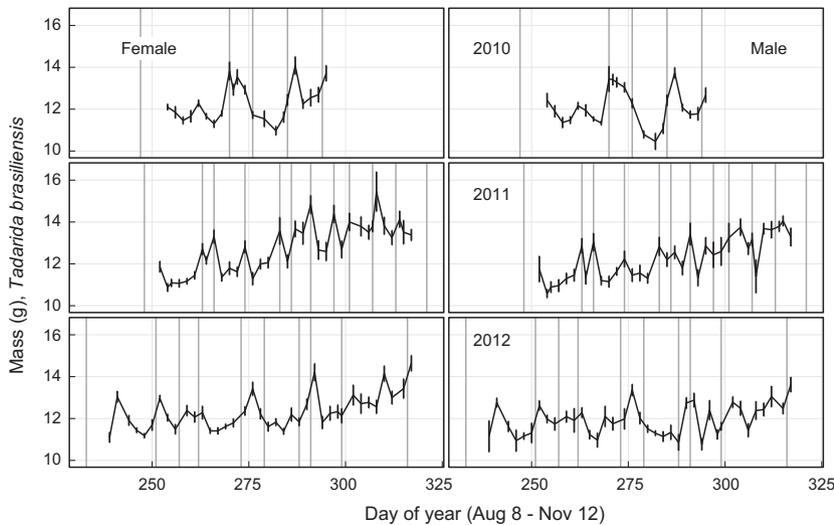
Fig. 3. Average bat mass (*Tadarida brasiliensis*) for males and females caught at Frio Cave, Uvalde Co., TX in 2010 (top), 2011 (middle) and 2012 (bottom). Error bars represent standard errors. Vertical grey lines represent day of cold front passage at Uvalde, TX.

Table 2. Models best explaining variation in duration of bat flight activity near Frio Cave, Uvalde Co., Texas in 2011, 2012 and both years combined. Temp = daily low temperature, Dew = daily low dew point, Wind = daily amount of northerly wind at night, Front = day of cold front passage at Uvalde, and B1, B2 = parameter represents the value of this variable the day before or 2 days before corresponding variation in duration of bat flight activity around Frio Cave, TX

Year	Parameters	Coefficients ± SE	Rel. Imp.	Model fit
2011	Bar**	-0.04 ± 0.015	0.130	Adj. $r^2 = 0.26$
	Dew*	0.02 ± 0.01	0.107	$F(3,55) = 7.80$
	Wind B2	0.01 ± 0.006	0.062	$P < 0.0002$
2012	Temp B1**	0.05 ± 0.016	0.104	Adj. $r^2 = 0.31$
	Wind	-0.02 ± 0.008	0.113	$F(4,70) = 10.06$
	Wind B1	0.02 ± 0.008	0.098	$P < 0.0001$
	Front*	0.60 ± 0.26	0.050	
All	Temp B1***	0.06 ± 0.01	0.158	Adj. $r^2 = 0.25$
	Wind B1***	0.02 ± 0.005	0.086	$F(3,130) = 15.78$
	Front**	0.40 ± 0.15	0.022	$P < 0.0001$
	Intercept*	-0.42 ± 0.18		

***$P < 0.001$, **$P < 0.01$, and *$P < 0.05$, $P < 0.10$.

gain $= 0.51 \pm 0.52$ g, $t = 2.092$, $P = 0.03$ and females: mean gain $= 0.80 \pm 0.48$ g, $t = 3.56$, $P = 0.003$).

Variables in linear regression models explained 26% of variation in duration of bat flight activity at Frio Cave (Table 2, Fig. 4) in 2011, 31% in 2012 and 25% with both years combined. Data were not available for 2010. Duration of bat flight activity increased with cold front passage the same day, and with increasing northerly wind and increasing low temperatures the previous day.

Discussion

Weather, especially at a synoptic or continental level, is an important factor in migration for many animals, including birds (Able 1973; Richardson 1990), bats (Krauel & McCracken 2013) and insects (Muller & Tucker 1986; Drake & Farrow 1988; Showers et al. 1993; Drake & Gatehouse 1995; Chapman et al. 2010, 2012). Weather patterns in this study showed a consistent trend of increasing northerly wind and decreasing temperature following local passage of cold fronts (Table S2, Supporting information), providing a mechanism for southward migration in autumn (Showers et al. 1993; Johnson 1995).

MOTHS

Corn earworm, the largest and most numerous noctuid moth species in this study (Table S1, Supporting information), is a migrant in both spring and autumn but is able to overwinter through diapause in the study area as well (Lopez et al. 1995; Westbrook & Lopez 2010). Fall armyworm is believed to be an obligate migrant due to an inability to diapause in cold climates (Johnson 1987; Nagoshi, Fleischer & Meagher 2009). Cabbage looper is also an obligate migrant and is intolerant of both extreme cold and heat (Franklin, Ritland & Myers 2011). Most cabbage looper studies are from the Pacific coast region, and little is known about its migratory patterns in the study area.

In our study, moth species showed a pattern of low numbers in late summer followed by sudden increases on or shortly after cold front passages. Both cabbage looper and fall armyworm numbers were lower in 2010 than later years, which may have been due to an unusually wet spring (King 1966; National Weather Service 2010a; a, Pair & Westbrook 1995). As in earlier studies (McCracken et al. 2012), there was a dramatic increase in the availability of corn earworm in mid-Sept, followed by a decline after the month's end (Fig. 2a–c). In general, fall armyworm and cabbage looper showed activity over a longer period and extending later into the season than did corn earworm (Fig. 2a–c). All moth species showed positive correlations with frontal passage or northerly wind. The College Station sites are 400 km northeast of the Uvalde sites (Fig. 1), and moths are thought to migrate
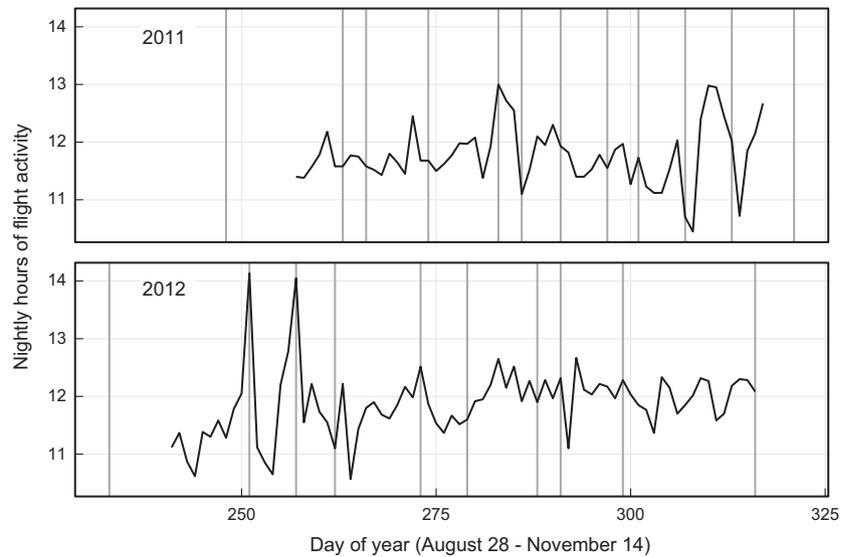
Fig. 4. Length of time bats were actively flying outside of Frio Cave, Uvalde Co., TX during the 2011 (upper) and 2012 (lower) autumn seasons, in hours, as measured by acoustic detectors placed adjacent to cave entrances. Vertical grey lines represent day of cold front passage at Uvalde, TX.

generally from northeast to southwest in autumn (Showers 1997), which would be supported by arrival at College Station earlier than at Uvalde. Fall armyworm moths did arrive 1 day earlier at College Station than at Uvalde (Table S4, Supporting information), but for other species there was not such a clear trend.

Our study provides evidence that all three noctuid moth species responded markedly to cold-front-related favourable weather patterns. These results support earlier work showing that noctuid moths migrate with cold fronts in autumn. Beerwinkle *et al.* (1994) observed large numbers of insects moving south in northerly winds after a cold front in Central Texas. Pair *et al.* (1987) reported a peak of migratory fall armyworm and corn earworm in Brownsville, Texas, 1–3 days after cold front passage in an area without host plants. Showers *et al.* (1993) dyed black cutworms and released them in Iowa when favourable northerly winds were expected; eight nights later, dyed moths were captured at College Station and one individual was recaptured in Brownsville. Our results also support findings of cold-front-driven migration in noctuid moths other parts of the world (Feng *et al.* 2009; Chapman *et al.* 2012). A similar pattern is also seen in other insects in North America; meteorological conditions associated with frontal systems stimulate emigrations of migrant potato leafhopper, *Empoasca fabae*, which would facilitate a return to their southern overwintering sites (Taylor & Reling 1986).

While the origin of moths caught in our pheromone traps is unknown, local corn earworms in Texas enter diapause in mid-September (Lopez & Hartstack 1985; Fitt 1989), and any increase in capture numbers likely represents migrants. Records from pheromone traps in potential migratory source locations (Fleischer *et al.* 2007) support this assertion. In all 3 years, cold front passages linked the end of moth activity north of Texas to spikes in moth numbers in Uvalde. Large numbers of corn earworm were caught in traps at Manhattan, Kansas, in

2010 until Sept 24, when a cold front travelled south into northern Texas (National Weather Service 2012a). The front stalled there until Sept 27, when it moved south over Uvalde, with a resulting spike in corn earworm in our traps. Corn earworm appeared at Manhattan traps until 25 Sept 2011, and a frontal system moved through there on Sept 24 followed by high pressure. The front reached Uvalde on Sept 27, followed by the season's highest corn earworm numbers 2 days later. In 2012, a series of frontal passages brought peak fall armyworm numbers to Iowa on Sept 13, 17 and 19, and fall armyworm numbers increased at Uvalde on Sept 20.

BAT MASS AND ACTIVITY

After producing and rearing pups, female Brazilian free-tailed bats are at their lowest fat levels in late August (O'Shea 1976, present study). High temperatures and parched vegetation likely contribute to reduced prey availability, as evidenced by the low numbers of moths in our pheromone traps at that time. Our study shows that average bat mass measured at the cave increases as migratory moths move through the area during autumn, especially in association with cold front passage, and mass variance increases over time in female bats.

The patterns we document in bat mass changes are from randomly selected individual bats; thus, differences in mass and mass variance are a proxy for proportional changes in the population of the cave on that date. Since we were not able to track changes in individual bats over time and bats may move between roosts especially in autumn (Krauel & McCracken 2013), these changes may also represent changes in overall cave population composition. Mass gain may be a direct result of consumption of migratory moths, although weight gain is likely to require more than a single night of foraging on high-fat-content prey. A more likely explanation for the observed patterns is the transition of Frio Cave from a

maternity roost in summer into a migratory stopover in autumn (Krauel & McCracken 2013). Frio Cave is located on the southernmost edge of the Edwards Plateau, a large karst area with many caves serving as roosts for free-tails and other bats (Short, Davis & Herreid 1960; Glass 1982). Migratory bats are known to take advantage of favourable wind associated with cold fronts (Cryan & Brown 2007). While we do not have data about bat population fluctuations at the cave during the study period, it was clear that numbers of bats returning to the cave increased dramatically on windy mornings after cold fronts. This is consistent with other reports showing that free-tailed bats change roosts with shifts in weather conditions in autumn (Svoboda & Choate 1987; Scales & Wilkins 2007; Hristov *et al.* 2010). Little is known about control of migratory onset in bats, although in many taxa, it is a combination of environmental cues and hormonally mediated thresholds (Ramenofsky & Wingfield 2007). Some bats are thought to undertake migration if they have accumulated sufficient fat reserves to complete the entire journey (McGuire *et al.* 2011). Our results may document the arrival of heavier bats moving south on favourable wind from more northerly roosts, producing changes in the population at Frio Cave. That is, females who spent the summer at the cave would be smaller than incoming migrants, and as the number of migrants increases, variance in mass as well as average mass overall should increase in conjunction with waves of new arrivals with cold fronts.

Duration of bat activity at the cave increased after cold fronts and with rising temperatures and increasing northerly wind. Our observations differed in two ways from those of previous studies conducted at Frio Cave earlier in the year (Lee & Kuo 2001; Reichard *et al.* 2009). First, the bats in our study generally left the cave at sunset throughout autumn, and differences in activity duration were primarily due to later returns at dawn, while previous studies showed variation in both daily departure and return time. Secondly, activity duration earlier in the year was linked to fluctuations in prey availability (Lee & Kuo 2001; Reichard *et al.* 2009), with activity time decreasing as moth abundance increased, a pattern consistent with bats requiring less time to meet foraging needs when prey is abundant. However, in this study, bat activity time increased with cold front passage rather than decreasing moth abundance. The difference in activity patterns, and the lack of a negative association between activity time and fluctuations in moth abundance, suggest that foraging needs may not drive variation in duration of activity at the cave in autumn. As with mass gain, the activity patterns we document may present further evidence of arrival of migrating bats. Bats using the cave as a stopover site might arrive on favourable wind later than resident bats returning from local foraging. The result would be consistent with our observation of increased duration of activity on those dates, especially on the first two cold fronts in the 2012 season.

Conclusions

Few integrative studies of migratory predators and their migratory prey are conducted across an entire migratory season (Chapman *et al.* 2006; Bowlin *et al.* 2010), and results confirm our hypothesis that the migratory process is primarily driven by weather (Shamoun-Baranes, Bouten & van Loon 2010). Understanding this particular study system is important for many reasons. Migratory moths incur considerable economic damage to crops, and bats provide important ecosystem services in control of those moths (Cleveland *et al.* 2006; Lopez-Hoffman *et al.* 2014). This overall system is driven by weather, which now faces unpredictable perturbations due to climate change.

The presence of migratory moths during a period of otherwise low resource availability may contribute substantially to the ability of free-tailed bats to undertake their own migrations. While the moths also use native vegetation (Lopez *et al.* 1995), the advent of human agriculture may have augmented moth migration and perhaps driven a northward range extension by the bats (Russell *et al.* 2011), allowing bats to take advantage of large cave systems in the study area. These important cave resources all along their migratory routes span international borders and thus represent a conservation challenge (Wiederholt *et al.* 2013; Berger *et al.* 2014).

Because weather is a primary factor in moth migration (Drake & Gatehouse 1995), and moth movements can reflect escapes from extremes of heat and cold (Showers 1997; Luo *et al.* 2002), climate change is likely to have a **3** marked impact on noctuid moth migration patterns (Parmesan 2001; Végvári *et al.* 2014). Extreme wet or dry conditions can have a large effect on noctuid moth migration (Pair & Westbrook 1995; present study), and a period of extended drought is already documented in the study area (National Weather Service 2012b). With fewer moths, bats may not gain enough mass to undertake their southward migrations, and be forced to overwinter in the area. If milder winters enable moths to remain in the area (Bale & Hayward 2010), the overwintering bats could be an important control mechanism. However, if overwintering corn earworm moths, the dominant moth in the study system, continue to enter diapause in late summer, they would be unavailable to the bats during this key period. Without a sufficient pulse of migrating moths, many bats may ultimately be forced to give up migration and remain in their wintering range, resulting in a marked decrease in available pest control services in the study area.

Our results may be applicable to other systems involving bats adapted for high-altitude foraging near corridors used by migratory insects (Drake & Gatehouse 1995; Fenton & Griffin 1997; Leelapaibul, Bumrungsri & Pattanawiboon 2005). Such systems may have enabled the evolution of social foraging (Dechmann *et al.* 2010), or permitted bats to migrate by providing sources of high-quality nutrition when little else is available. Additionally, high-flying social bats found in areas supporting insect

migrations are often migrants themselves (Krauel & McCracken 2013). Integrative studies of animal migration are difficult, but provide important insights into complex relationships facing a variety of threats (Bowlin *et al.* 2010; Bauer & Hoye 2014).

Acknowledgements

Data accessibility

Data are available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.0h160 (Krauel, Westbrook & McCracken 2014).

References

Able, K.P. (1973) Role of weather variables and flight direction in determining magnitude of nocturnal bird migration. *Ecology*, **54**, 1031–1041.

Alerstam, T., Chapman, J.W., Bäckman, J., Smith, A.D., Karlsson, H.K., Nilsson, C. *et al.* (2011) Convergent patterns of long-distance nocturnal migration in noctuid moths and passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, **????**, ????–????. [4]

Bairlein, F. (2002) How to get fat: nutritional mechanisms of seasonal fat accumulation in migratory songbirds. *Naturwissenschaften*, **89**, 1–10.

Bale, J.S. & Hayward, S.A.L. (2010) Insect overwintering in a changing climate. *Journal of Experimental Biology*, **213**, 980–994.

Bauer, S. & Hoye, B.J. (2014) Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, **344**, 1242552.

Beerwinkle, K.R., Lopez, J.D., Witz, J.A., Schleider, P.G., Eyster, R.S. & Lingren, P.D. (1994) Seasonal radar and meteorological observations associated with nocturnal insect flight at altitudes to 900 meters. *Environmental Entomology*, **23**, 676–683.

Berger, J., Cain, S.L., Cheng, E., Dratch, P., Ellison, K., Francis, J. *et al.* (2014) Optimism and challenge for science-based conservation of migratory species in and out of U.S. National Parks. *Conservation Biology*, **28**, 4–12.

Betke, M., Hirsh, D.E., Makris, N.C., McCracken, G.F., Procopio, M., Hristov, N.I. *et al.* (2008) Thermal imaging reveals significantly smaller Brazilian free-tailed bat colonies than previously estimated. *Journal of Mammalogy*, **89**, 18–24.

Bowlin, M.S., Bisson, I.-A., Shamoun-Baranes, J., Reichard, J.D., Sapir, N., Marra, P.P. *et al.* (2010) Grand challenges in migration biology. *Integrative and Comparative Biology*, **50**, 261–279.

Chapman, J.W., Drake, V.A. & Reynolds, D.R. (2011) Recent insights from radar studies of insect flight. *Annual Review of Entomology*, **56**, 337–356.

Chapman, J.W., Reynolds, D.R., Brooks, S.J., Smith, A.D. & Woiwod, I.P. (2006) Seasonal variation in the migration strategies of the green lacewing *Chrysoperla carnea* species complex. *Ecological Entomology*, **31**, 378–388.

Chapman, J.W., Reynolds, D.R., Mouritsen, H., Hill, J.K., Riley, J.R., Sivell, D. *et al.* (2008) Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Current Biology*, **18**, 514–518.

Chapman, J.W., Nesbit, R.L., Burgin, L.E., Reynolds, D.R., Smith, A.D., Middleton, D.R. *et al.* (2010) Flight orientation behaviors promote optimal migration trajectories in high-flying insects. *Science*, **327**, 682–685.

Chapman, J.W., Bell, J.R., Burgin, L.E., Reynolds, D.R., Pettersson, L.B., Hill, J.K. *et al.* (2012) Seasonal migration to high latitudes results in major reproductive benefits in an insect. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 14924–14929.

Cleveland, C.J., Betke, M., Federico, P., Frank, J.D., Hallam, T.G., Horn, J. *et al.* (2006) Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. *Frontiers in Ecology and the Environment*, **5**, 238–243.

Cryan, P.M. & Brown, A.C. (2007) Migration of bats past a remote island offers clues toward the problem of bat fatalities at wind turbines. *Biological Conservation*, **139**, 1–11.

Dechmann, D.K.N., Heucke, S.L., Giuggioli, L., Safi, K., Voigt, C.C. & Wikelski, M. (2009) Experimental evidence for group hunting via eavesdropping in echolocating bats. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 2721–2728.

Dechmann, D.K.N., Kranstauber, B., Gibbs, D. & Wikelski, M. (2010) Group hunting-a reason for sociality in Molossid bats? *PLoS One*, **5**, 2.

DeLurgio, S.A. (1998) *Forecasting Principles and Applications*. Irwin/McGraw-Hill College, Boston, Massachusetts, USA.

Dingle, H. (2014) *Migration: The Biology of Life on the Move*. Oxford University Press, New York, New York, USA.

Domino, R.P., Showers, W.B., Taylor, S.E. & Shaw, R.H. (1983) Spring weather pattern associated with suspected black cutworm moth (Lepidoptera, Noctuidae) introduction to Iowa. *Environmental Entomology*, **12**, 1863–1872.

Drake, V.A. & Farrow, R.A. (1988) The influence of atmospheric structure and motions on insect migration. *Annual Review of Entomology*, **33**, 183–210.

Drake, V.A. & Gatehouse, A.G. (eds.) (1995) *Insect Migration: Tracking Resources Through Space and Time*. Cambridge University Press, Cambridge.

Drake, V.A. & Reynolds, D.R. (eds.) (2012) *Radar Entomology: Observing Insect Flight and Migration*. CABI, Wallingford.

Feng, H.Q., Wu, K.M., Cheng, D.F. & Guo, Y.Y. (2003) Radar observations of the autumn migration of the beet armyworm *Spodoptera exigua* (Lepidoptera: Noctuidae) and other moths in northern China. *Bulletin of Entomological Research*, **93**, 115–124.

Feng, H.Q., Wu, X.F., Wu, B. & Wu, K.M. (2009) Seasonal migration of *Helicoverpa armigera* (Lepidoptera: Noctuidae) over the Bohai Sea. *Journal of Econonomic Entomology*, **102**, 95–104.

Fenton, M.B. & Griffin, D.R. (1997) High-altitude pursuit of insects by echolocating bats. *Journal of Mammalogy*, **78**, 247–250.

Fitt, G.P. (1989) The ecology of *Heliothis* species in relation to agroecosystems. *Annual Review of Entomology*, **34**, 17–52.

Fleischer, S., Payne, G., Kuhar, T., Herbert, A. Jr, Malone, S., Whalen, J. *et al.* (2007) *Helicoverpa zea* trends from the Northeast: suggestions towards collaborative mapping of migration and pyrethroid susceptibility. *Plant Health Progress*, **????**, ????–????. [5]

Franklin, M.T., Ritland, C.E. & Myers, J.H. (2011) Genetic analysis of cabbage loopers, *Trichoplusia ni* (Lepidoptera: Noctuidae), a seasonal migrant in western North America. *Evolutionary Applications*, **4**, 89–99.

Gillam, E.H. (2007) Eavesdropping by bats on the feeding buzzes of conspecifics. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **85**, 795–801.

Glass, B.P. (1982) Seasonal movements of Mexican freetail bats *Tadarida-brasiliensis*-mexicana banded in the great plains. *Southwestern Naturalist*, **27**, 127–133.

Gould, F., Blair, N., Reid, M., Rennie, T.L., Lopez, J. & Micinski, S. (2002) *Bacillus thuringiensis*-toxin resistance management: Stable isotope assessment of alternate host use by *Helicoverpa zea*. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 16581–16586.

Gregg, P.C., Fitt, G.P., Coombs, M. & Henderson, G.S. (1994) Migrating moths collected in tower-mounted light traps in northern New-South-Wales, Australia - influence of local and synoptic weather. *Bulletin of Entomological Research*, **84**, 17–30.

Grömping, U. (2006) Relative importance for linear regression in R: the package relaimpo. *Journal of Statistical Software*, **17**, 1–27.

Hein, A.M., Hou, C. & Gillooly, J.F. (2012) Energetic and biomechanical constraints on animal migration distance. *Ecology Letters*, **15**, 104–110.

Hill, D.S. (2008) *Pests of Crops in Warmer Climates and Their Control*. Springer Science + Business Media, Berlin.

Hristov, N.I., Betke, M., Theriault, D.E.H., Bagchi, A. & Kunz, T.H. (2010) Seasonal variation in colony size of Brazilian free-tailed bats at Carlsbad Cavern based on thermal imaging. *Journal of Mammalogy*, **91**, 183–192.

Johnson, S.J. (1987) Migration and the life-history strategy of the fall armyworm, *Spodoptera-frugiperda* in the Western Hemisphere. *Insect Science and Its Application*, **8**, 543–549.

Johnson, S. (1995) Insect migration in North America: synoptic-scale transport in a highly seasonal environment. *Insect Migration: Tracking Resources through Space and Time*. (eds V.A. Drake & A.G. Gatehouse), pp 31–66. Cambridge University Press, Cambridge.

King, E.W. (1966) Rainfall temperature and population levels of certain South Carolina lepidoptera I. *Trichoplusia ni. Annals of the Entomological Society of America*, **59**, 1049–1055.

Krauel, J.J. & McCracken, G.F. (2013) Recent advances in bat migration research. *Bat Evolution, Ecology, and Conservation*. (eds R.A. Adams & S.C. Pedersen), pp 293–314. Springer Science Press, New York, New York, USA.

Krauel, J.J., Westbrook, J.K. & McCracken, G.F. (2014) Data from: Weather-driven dynamics in a dual-migrant system: moths and bats. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.0 h160.

Lee, Y.F. & Kuo, Y.M. (2001) Predation on Mexican free-tailed bats by Peregrine Falcons and Red-tailed Hawks. *Journal of Raptor Research*, **35**, 115–123.

Lee, Y.F. & McCracken, G.F. (2002) Foraging activity and food resource use of Brazilian free-tailed bats, *Tadarida brasiliensis* (Molossidae). *Ecoscience*, **9**, 306–313.

Lee, Y.F. & McCracken, G.F. (2005) Dietary variation of Brazilian free-tailed bats links to migratory populations of pest insects. *Journal of Mammalogy*, **86**, 67–76.

Lee, T.R., De Wekker, S.F.J., Andrews, A.E., Kofler, J. & Williams, J. (2012) Carbon dioxide variability during cold front passages and fair weather days at a forested mountaintop site. *Atmospheric Environment*, **46**, 405–416.

Leelapaibul, W., Bumrungsri, S. & Pattanawiboon, A. (2005) Diet of wrinkle-lipped free-tailed bat (*Tadarida plicata* Buchannan, 1800) in central Thailand: insectivorous bats potentially act as biological pest control agents. *Acta Chiropterologica*, **7**, 111–119.

Legendre, P. & Legendre, L. (2012) . *Numerical Ecology. Developments in Environmental Modeling*, vol. 24. Elsevier, Oxford.

Leskinen, M., Markkula, I., Koistinen, J., Pylkkö, P., Ooperi, S., Siljamo, P. et al. (2011) Pest insect immigration warning by an atmospheric dispersion model, weather radars and traps. *Journal of Applied Entomology*, **135**, 55–67.

Lopez, J.D. Jr & Hartstack, A.W. Jr (1985) Comparison of diapause development in *Heliothis zea* and *H. virescens* (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America*, **78**, 415–422.

Lopez, J.D., Beerwinkle, K.R., Witz, J.A. & Goodenough, J.L. (1995) Spatial and temporal patterns of catches in pheromone traps of *Helicoverpa-zea* Lepidoptera, Noctuidae and *Heliothis-virescens* Lepidoptera, Noctuidae in Central Texas. *Southwestern Entomologist*, **????**, 5–24. [6]

Lopez-Hoffman, L., Wiederholt, R., Sansone, C., Bagstad, K.J., Cryan, P., Diffendorfer, J.E. et al. (2014) Market forces and technological substitutes cause fluctuations in the value of bat pest-control services for cotton. *PLoS One*, **9**, 2.

Luo, L.Z., Johnson, S.J., Hammond, A.M., Lopez, J.D., Geaghan, J.P., Beerwinkle, K.R. et al. (2002) Determination and consideration of flight potential in a laboratory population of true armyworm (Lepidoptera: Noctuidae). *Environmental Entomology*, **31**, 1–9.

McCracken, G.F., Gillam, E.H., Westbrook, J.K., Lee, Y.F., Jensen, M.L. & Balsley, B.B. (2008) Brazilian free-tailed bats (*Tadarida brasiliensis*: Molossidae, Chiroptera) at high altitude: links to migratory insect populations. *Integrative & Comparative Biology*, **48**, 107–118.

McCracken, G.F., Westbrook, J.K., Brown, V.A., Eldridge, M., Federico, P. & Kunz, T.H. (2012) Bats track and exploit changes in insect pest populations. *PLoS One*, **7**, 8.

McGuire, L.P., Guglielmo, C.G., Mackenzie, S.A. & Taylor, P.D. (2011) Migratory stopover in the long-distance migrant silver-haired bat, *Lasionycteris noctivagans*. *Journal of Animal Ecology*, **81**, 385–394.

McNeil, J.N. (1987) The true armyworm, *Pseudaletia-unipuncta* - a victim of the pied piper or a seasonal migrant. *Insect Science and Its Application*, **8**, 591–597.

Muller, R.A. & Tucker, N.L. (1986) Climatic opportunities for the long-range migration of moths. *Long-range Migration of Moths of Agronomic Importance to the United States and Canada: Specific Examples of Occurrence and Synoptic Weather Patterns Conducive to Migration*. (ed A.N. Sparks), pp. 61–83. USDA-ARS, ????. [7]

Nagoshi, R.N., Fleischer, S. & Meagher, R.L. (2009) Texas is the overwintering source of fall armyworm in Central Pennsylvania: implications for migration into the Northeastern United States. *Environmental Entomology*, **38**, 1546–1554.

National Weather Service. 2010–2012a. Daily Surface Weather Map. National Centers for Environmental Prediction. http://www.hpc.ncep.noaa.gov/dailywxmap.

National Weather Service. 2010–2012b. Weather Summary, Brownsville Texas. http://www.srh.noaa.gov/bro/?n = 2010event_annualsummary.

Newton, I. (2008) *The Migration Ecology of Birds*. Elsevier Academic Press Inc, San Diego, California, USA.

O'Shea, T.J. (1976) Fat content in migratory central Arizona Brazilian free-tailed bats *Tadarida-brasiliensis* Molossidae. *Southwestern Naturalist*, **21**, 321–326.

Overington, S.E., Dubois, F. & Lefebvre, L. (2008) Food unpredictability drives both generalism and social foraging: a game theoretical model. *Behavioral Ecology*, **19**, 836–841.

Pair, S.D. & Westbrook, J.K. (1995) Agroecological and climatological factors potentially influencing armyworm Lepidoptera, Noctuidae populations and their movement in the Southeastern United-States. *Southwestern Entomologist*, **????**, 101–118. [8]

Pair, S.D., Raulston, J.R., Rummel, D.R., Westbrook, J.K., Wolf, W.W., Sparks, A.N. et al. (1987) Development and production of corn-earworm (Lepidoptera, Noctuidae) and fall armyworm (Lepidoptera, Noctuidae) in the Texas High-Plains - evidence for reverse fall migration. *Southwestern Entomologist*, **12**, 89–99.

Pair, S.D., Raulston, J.R., Sparks, A.N., Westbrook, J.K., Wolf, W.W. & Goodenough, J.L. (1995) A prospectus - Impact of *Helicoverpa-zea* Lepidoptera, Noctuidae (Boddie) production from corn in the Lower Rio-Grande Valley on regional cropping systems. *Southwestern Entomologist*, **????**, 155–167. [9]

Parmesan, C. (2001) Coping with modern times? Insect movement and climate change. *Insect Movement: Mechanisms and Consequences. Proceedings of the Royal Entomological Society's 20th Symposium* (eds I.P. Woiwod, D.R. Reynolds & C.D. Thomas), pp 387–413. ?????, London, September 1999. [10]

R Development Core Team. (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.

Ramenofsky, M. & Wingfield, J.C. (2007) Regulation of migration. *BioScience*, **57**, 135–143.

Rankin, M.A. & Burchsted, J.C.A. (1992) the cost of migration in insects. *Annual Review of Entomology*, **37**, 533–559.

Ratcliffe, J.M. & ter Hofstede, H.M. (2005) Roosts as information centres: social learning of food preferences in bats. *Biology Letters*, **1**, 72–74.

Reichard, J.D., Gonzalez, L.E., Casey, C.M., Allen, L.C., Hristov, N.I. & Kunz, T.H. (2009) Evening emergence behavior and seasonal dynamics in large colonies of Brazilian Free-Tailed Bats. *Journal of Mammalogy*, **90**, 1478–1486.

Richardson, W.J. (1990). *Timing of Bird Migration in Relation to Weather: Updated Review. Bird Migration: Physiology and Ecophysiology*. Springer-Verlag, Berlin.

Russell, A.L., Cox, M.P., Brown, V.A. & McCracken, G.F. (2011) Population growth of Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) predates human agricultural activity. *Bmc Evolutionary Biology*, **11**, 88.

Scales, J.A. & Wilkins, K.T. (2007) Seasonality and fidelity in roost use of the Mexican free-tailed bat, *Tadarida brasiliensis*, in an urban setting. *Western North American Naturalist*, **67**, 402–408.

Shamoun-Barnes, J., Bouten, W. & van Loon, E.E. (2010) Integrating meteorology into research on migration. *Integrative & Comparative Biology*, **50**, 280–292.

Short, H.L., Davis, R.B. & Herreid, C.F. (1960) Movements of the Mexican free-tailed bat in Texas. *Southwestern Naturalist*, **5**, 208–216.

Showers, W.B. (1997) Migratory ecology of the black cutworm. *Annual Review of Entomology*, **42**, 393–425.

Showers, W.B., Whitford, F., Smelser, R.B., Keaster, A.J., Robinson, J.F., Lopez, J.D. et al. (1989) Direct evidence for meteorologically driven long-range dispersal of an economically important moth. *Ecology*, **70**, 987–992.

Showers, W.B., Keaster, A.J., Raulston, J.R., Hendrix, W.H., Derrick, M.E., McCorcle, M.D. et al. (1993) Mechanism of southward migration of a noctuid moth [*Agrotis-ipsilon* (Hufnagel)] - a complete migrant. *Ecology*, **74**, 2303–2314.

Svoboda, P.L. & Choate, J.R. (1987) Natural-History of the Brazilian free-tailed bat in the San Luis Valley of Colorado. *Journal of Mammalogy*, **68**, 224–234.

Taylor, R.A.J. & Reling, D. (1986) Preferred wind direction of long-distance leafhopper (*Empoasca fabae*) migrants and its relevance to the return migration of small insects. *Journal of Animal Ecology*, **55**, 1103–1114.

Triplehorn, C.A. & Johnson, N.F. (2005) *Borror and DeLong's Introduction to the Study of Insects*, 7th edn. Thompson Brooks/Cole, Belmont, California, USA.

Végvári, Z., Juhász, E., Tóth, J.P., Barta, Z., Boldogh, S., Szabó, S. *et al.* (2014) Life-history traits and climatic responsiveness in noctuid moths. *Oikos*, **????**, ????–????. doi:10.1111/oik.01655.

Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York, New York, USA.

Westbrook, J.K. & Lopez, J.D. (2010) Long-distance migration in *Helicoverpa zea*: what we know and need to know. *Southwestern Entomologist*, **35**, 355–360.

Wiederholt, R., Lopez-Hoffman, L., Cline, J., Medellin, R.A., Cryan, P., Russell, A. *et al.* (2013) Moving across the border: modeling migratory bat populations. *Ecosphere*, **4**, art114.

Wilkins, K.T. (1989) *Tadarida-Brasiliensis. Mammalian Species*, **331**, 1–10.

Wilkinson, G.S. (1992) information-transfer at evening bat colonies. *Animal Behavior*, **44**, 501–518.

Yang, L.H., Bastow, J.L., Spence, K.O. & Wright, A.N. (2008) What can we learn from resource pulses? *Ecology*, **89**, 621–634.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. (a–c) Median moth captures by species at pheromone traps at both the Uvalde (UV) and College Station (CS) sites in (a) 2010, (b) 2011, and (c) 2012.

Table S1. Total number of moths caught in all pheromone trap replicates by moth species, year, and site (Uvalde and College Station, TX).

Table S2. Statistically significant cross-correlations between meteorological variables and passage of cold fronts or hours of nightly wind at Uvalde, TX.

Table S3. Complete list of statistically significant cross-correlations between moth abundance and weather variables.

Table S4. Statistically significant cross-correlations between moth abundances at Uvalde and College Station sites.