Temporal Changes in Body Mass and Body Condition of Cave-Hibernating Bats During Staging and Swarming

Michael J. Lacki,* Luke E. Dodd, Rickard S. Toomey, Steven C. Thomas, Zachary L. Couch, Barry S. Nichols

M.J. Lacki
Department of Forestry, University of Kentucky, Lexington, Kentucky 40546

L.E. Dodd
Department of Biological Sciences, Eastern Kentucky University, Richmond, Kentucky 40475

R.S. Toomey, S.C. Thomas
National Park Service, Mammoth Cave National Park, Mammoth Cave, Kentucky 42259

Z.L. Couch
Kentucky Department for Environmental Protection, Division of Water, Frankfort, Kentucky 40601

B.S. Nichols
P.O. Box 21182, Louisville, Kentucky 40221

Abstract

The rapid colonization of the *Pseudogymnoascus destructans* fungus across cave systems in eastern North America and the associated bat mortalities (white-nose syndrome; WNS), necessitates studies of cave-hibernating bats that remain unaffected by, or in close proximity to, the leading edge of the fungal distribution to provide baseline predisturbance data from which to assess changes due to fungal effects. Studies of the physiological ecology of cave-hibernating bats during the spring staging and autumn swarming seasons are few, and an understanding of patterns in body condition of bats associated with entry into and emergence from hibernation is incomplete. We sampled bats at the entrance to a cave in Mammoth Cave National Park, Kentucky, during swarming and staging, prior to (2011 and 2012), concurrent with (2013), and following (2014) the arrival of the WNS fungus. We evaluated seasonal and annual changes in body mass and body condition of bats entering and leaving the cave. We captured 1,232 bats of eight species. Sex ratios of all species were male-biased. Capture success was substantially reduced in 2014, following the second winter after arrival of the WNS fungus. Significant temporal variation in body mass and body mass index was observed for little brown bats *Myotis lucifugus,* northern long-eared bats *M. septentrionalis,* and tri-colored bats *Perimyotis subflavus,* but not Indiana bats *M. sodalis*. Little brown bats and northern long-eared bats demonstrated significant increases in mean body mass index in 2014; this pattern likely reflected a relatively better body condition in bats that survived exposure to the WNS fungus. Most species demonstrated highest body mass and body mass index values in late swarming compared with other sampling periods, with tri-colored bats showing the greatest percent increase in body mass (42.5%) and body mass index (42.9%) prior to entering hibernation. These data indicate significant intraspecific variation in body condition of cave-hibernating bat species, both among years and between the seasons of autumn swarming and spring staging. We suggest this variation is likely to have implications for the relative vulnerability of species to WNS infection across the distribution of the *Pseudogymnoascus* fungus.

Keywords: bats; body mass; hibernation; staging; swarming; white-nose syndrome

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* Corresponding author: mlacki@uky.edu

Introduction

Bats in the northern temperate zone face energetic stressors in winter months because of cold ambient temperatures. These conditions lead to reduced availability of insect prey and higher metabolic costs of thermoregulation, forcing species to choose between migration in autumn to warmer climates (Fleming and Eby 2003; Cryan and Veilleux 2007) or moving shorter distances at the completion of the breeding season to roosting sites nearby and entering periods of deep torpor or hibernation (Speakman and Thomas 2003). Winter hibernation is preceded by autumn swarming, when breeding occurs and when bats accumulate fat reserves, and is followed by spring staging, when bats disperse to summer activity areas and maternity sites. During autumn swarming, bats must build fat stores to sustain them through winter hibernation. Estimates suggest little brown bats *Myotis lucifugus* need to add up to 2.3 g of fat to sustain hibernation periods that can last up to 9 mo at more northern latitudes (Kunz et al. 1998). Accumulation of fat reserves for hibernation is slowed by the energy expended in mating behaviors and flight (Piksa 2008; Šuba et al. 2011). Evidence suggests males in poorer body condition often spend more time in swarming activities than presumably healthier males in better condition (Lowe 2012).

Autumn swarming is associated with rapid flight, chasing behavior, and vocalizations of large numbers of bats in and around the entrances to caves (Fenton 1969; Thomas et al. 1979; Furmankiewicz et al. 2013). Most typically associated with *Myotis* bats, swarming is known to occur in seven genera of Microchiropteran bats (Parsons et al. 2003). This behavior begins in late summer, peaks in mid-autumn, and ceases in mid-October to early November when bats enter hibernation (Šuba et al. 2008; Vintulis and Šuba 2010). Swarming is hypothesized to serve several functions, including finding mates (Parsons et al. 2003; Rivers et al. 2005), introducing volant young to hibernation sites (Humphrey and Cope 1976; Veith et al. 2004), serving as rendezvous sites in migration (Fenton 1969), and assessing conditions inside hibernacula (Davis and Hitchcock 1965; Furmankiewicz and Górniak 2002). Sex ratios of swarming bats are usually male-biased (Piksa 2008; Šuba et al. 2008; Vintulis and Šuba 2010), although exceptions have been reported for the greater mouse-eared bat *Myotis myotis* (Pocora et al. 2012). Swarming behavior can facilitate gene flow, especially among relatively isolated summer colonies of bats (Kerth et al. 2003; Veith et al. 2004; Rivers et al. 2006). Male-biased hybridization is also known to occur among species during autumn swarming, suggesting at least some randomness in mating during swarming and therefore high evolutionary potential for speciation and biodiversity (Bogdanowicz et al. 2012).

Less is known about the spring staging or transient season (Neubaum et al. 2014). Females are believed to awaken and emerge from hibernacula earlier in spring than males (Cope and Humphrey 1977; Little and Brack 2001), with some males remaining at hibernacula well into the summer (Hall 1962; Whitaker and Brack 2001). Both male- and female-biased sex ratios have been reported for bats during spring staging (Little and Brack 2001). Mating is believed to occur throughout hibernation and into the spring staging season, but to a lesser extent than observed during autumn swarming (Thomas et al. 1979; Wai-Ping and Fenton 1988; Watt and Fenton 1995). The relative importance of copulations in autumn versus spring is still unclear (Burland et al. 2001; Senior et al. 2005). Regardless, during spring staging, temperate zone bats must build fat reserves to support pregnancy and the gestation of young (Speakman and Thomas 2003).

The arrival of the fungus *Pseudogymnoascus destructans* to cave systems in North America in 2006 has led to widespread mortality of cave-roosting bats (USFWS 2012). The debilitating effects of the fungus (Frick et al. 2010), now known as white-nose syndrome (WNS), have created concern for the long-term conservation of cave-hibernating bats in eastern North America. Mortality of bats at hibernacula in eastern North America likely exceed the estimated 6.7 million deaths reported since 2007 (USFWS 2012) and, despite efforts to ensure that humans do not spread the fungus among caves (Shelley et al. 2013), the fungus continues to expand in distribution and has now been detected on 12 species of bats over multiple states and Canadian provinces (https://www.whitenosesyndrome.org).

For bats that successfully reach the spring staging season, WNS can cause significant tissue damage to wing membranes (Reichard and Kunz 2009). The degree of recovery from injuries following spring staging (i.e., measured reduction in wing-damaged area between initial and recapture samples) correlates with body mass index (BMI), and on average, individuals with higher BMI in late spring and early summer have less overall wing damage (Fuller et al. 2011). Thus, replacing fat stores during spring staging is likely important to survival and reproduction of bats emerging from hibernation, especially individuals affected by WNS. In this study, we monitored BMI and body mass of bats during autumn swarming and spring staging from 2011 to 2014 at a cave entrance in Mammoth Cave National Park, Kentucky, before, during, and after the arrival of WNS to the Park. We hypothesized that 1) BMI and body mass would vary across seasons with individuals achieving highest levels in late swarming, just prior to hibernation, and lowest levels in early staging, immediately following hibernation; and 2) annual changes in BMI and body-mass levels would be associated with survival of bats following exposure to WNS, resulting in higher mean values of BMI and body mass after arrival of the WNS fungus to the Park.

Methods

Study area

Mammoth Cave National Park consists of 23,000 ha in Barren, Hart, and Edmonson counties (37.2072°N, 86.1319°W) of central Kentucky, on the edge of the Crawford–Mammoth Cave Uplands of the Interior Plateau (Woods et al. 2002). The Park is largely forested and supports primarily oak–hickory *Quercus*–*Carya* spp. and western mixed mesophytic forests (Braun 1950). Management of forests at Mammoth Cave National Park includes use of prescribed fire to restore historic native plant communities, with fires set during spring seasons from 2004 through 2010. Roughly 33% of the Park land surface was burned 1 or 2 times during this 7-y interval, creating available foraging habitats for bats ranging from unburned to 7 y postburn at the start of this study.

Erosion of limestone and sandstone bedrock by numerous drainage systems has produced a topographically diverse landscape containing hundreds of caves, including the longest known cave system in the world. We captured bats at the entrance of Colossal Cave, a Priority 2 hibernaculum (i.e., habitat that contributes to the recovery and long-term conservation of the species) for the Indiana bat *Myotis sodalis* (USFWS 2007). Colossal Cave is a portion of the Mammoth Cave system that received commercial use in the late 1800s, and the entrance where we captured bats was an artificial access point that was created to allow entry into the cave by tour groups. Evidence reflecting prior commercial use remains, with entry now restricted by an angle iron gate and signage. White-nose syndrome was first confirmed in the Park in February 2013 on a northern long-eared bat *M. septentrionalis,* and was discovered in Colossal Cave later that winter.

Sampling approach

We captured bats at Colossal Cave using a harp trap placed at the cave entrance, with the surrounding flight space enclosed with netting to ensure that exiting bats passed through the trap wires. The trap was set for six nights in each of 2011, 2012, and 2013, and for seven nights in 2014. One capture night in spring 2014 (4 April) produced only a single bat, so we added an extra capture night to ensure more sampled individuals. Over the 4 y of sampling, we conducted three trapping nights during autumn swarming from 21 August to 3 October (44-d period) and during spring staging from 5 April to 20 May (45-d sampling period). Actual trap dates varied among years because of weather, logistics, and personnel availability; regardless, we attempted to distribute sampling nights roughly 2–3 wk apart to ensure wide coverage of the extent of the staging and swarming seasons each year. Thus, within each season the three sample nights represent early, mid-, and late-swarming (late August–early September [SW1], mid-September [SW2], and late September–early October [SW3]) and early, mid-, and late-staging (early April [ST1], mid- to late April [ST2], and early to mid-May [ST3]), respectively. On each sampling night, we operated the trap from dusk until approximately 2300 hours, or until we captured 50–60 bats; the nightly catch limit restriction was mandated in the study protocol approved by the University of Kentucky Institutional Animal Care and Use Committee (IACUC No. 2010-0660).

We followed all national WNS protocols for operating, disinfecting, and cleaning trapping equipment and for the handling of bats to prevent the spread of fungal spores among bats and humans (http://www.whitenosesyndrome.org). We placed bats into separate decontaminated cloth bags and then identified them to species. For each bat, we collected the following: 1) mass (g) using a digital scale; 2) age based on fusion of the finger joints (adult vs. juvenile; Brunet-Rossinni and Wilkinson 2009); 3) right forearm length (mm), measured with digital calipers; 4) sex; 5) reproductive condition assessed by examining development of the epididymes (males) or the presence of a fetus, swollen vulva, or swollen teats (females; Racey 2009); 6) wing damage (wing damage index [WDI] scale: 0—no damage; 1—$<$50% of membrane as scar tissue; 2—$>$50% of membrane as scar tissue; 3—necrotic tissue with $>$0.5-cm holes; Reichard and Kunz 2009); 7) presence of lesions on wing membranes, which were scanned with ultraviolet light (Turner et al. 2014); and 8) presence of external parasites. We fitted *Myotis* spp. bats with a 2.9-mm identification arm band (bands supplied by Kentucky Department of Fish and Wildlife Resources, Frankfort, KY) prior to releasing bats.

Statistical analyses

We calculated sex ratios (males/female) for all species captured. We plotted capture success of bats (number of bats/trap-hour) by species across seasons and years to evaluate numerical trends in relation to the arrival of WNS to the cave. We generated body condition indices (BMI) as body mass (g)/right forearm length (mm; Pearce et al. 2008). We calculated mean body mass (g), right forearm length (mm), and BMI for each species captured. We assessed temporal patterns in the percentage of bats differing in WDI scores and the percentage of bats with lesions on wing membranes (UV Scan). For species with sufficient sample size ($n > 80$ bats), we assessed variation in body mass and BMI by modeling the effects of sampling period (early, mid-, and late swarming; and early, mid-, and late staging), year (2011, 2012, 2013, and 2014), and sampling period $\times$ year interaction with a multiway analysis of variance. We evaluated effect sizes using Type III Sums of Squares because of unbalanced sample sizes across cells (Pendleton et al. 1986). We compared mean body mass and BMI across years and sampling periods for each species. All statistical procedures were run in SAS (SAS Inc. 2002). For all statistical analyses, an effect was interpreted as significant when $P < 0.05$.

Results

We captured 1,232 bats of eight species in harp traps from 2011 to 2014 (Tables S1-S3, *Supplemental Material*). Tri-colored bats *Perimyotis subflavus* and northern long-eared bats were the most abundant species, representing 83.7% of the total captures collectively (Table 1).

Table 1. Species, sex ratios, and numbers of bats captured at Colossal Cave, Mammoth Cave National Park, Kentucky, 2011 to 2014, including mean (±SD) body mass (g), right forearm length (mm), and body mass index (BMI: g/mm).

Species	*n*	Sex ratio (male:female)	Body mass (g)	Forearm length (mm)	BMI (g/mm)
Perimyotis subflavus (tri-colored bat)	598	2.93:1.0	5.11 ± 0.97	34.1 ± 1.18	0.15 ± 0.03
Myotis septentrionalis (northern long-eared bat)	433	3.42:1.0	5.69 ± 0.76	35.6 ± 1.27	0.16 ± 0.02
Myotis lucifugus (little brown bat)	83	4.6:1.0	6.78 ± 0.94	37.3 ± 1.33	0.18 ± 0.02
Myotis sodalis (Indiana bat)	82	7.2:1.0	6.68 ± 0.65	38.9 ± 1.28	0.17 ± 0.02
Myotis leibii (eastern small-footed bat)	19	3.75:1.0	4.07 ± 0.4	30.0 ± 0.77	0.14 ± 0.01
Corynorhinus rafinesquii (Rafinesque's big-eared bat)	9	Males only	9.79 ± 0.63	43.5 ± 1.05	0.22 ± 0.01
Eptesicus fuscus (big brown bat)	5	4.0:1.0	19.1 ± 2.82	48.6 ± 1.37	0.39 ± 0.06
Lasiurus borealis (eastern red bat)	3	2.0:1.0	9.48 ± 0.58	39.8 ± 0.65	0.24 ± 0.02

All species captured demonstrated male-biased sex ratios. Juveniles comprised 8.56% of the bats captured during swarming, with this value likely an underestimate of juveniles in the samples because of ossification of the finger bones in some individuals by the mid- and late swarming periods causing us to incorrectly age some juveniles as adults. Capture rates of bats were largely consistent across the first 3 y of sampling, with capture rates declining precipitously in 2014 (Figure 1). Both species that were abundant in the cave prior to WNS—the northern long-eared bat and tri-colored bat—demonstrated marked declines in capture rates in 2014 sampling periods.

Bats with WDI scores of 1 and 2 represented 10.1% and 0.26% of all bats captured, respectively; no bat was assigned a WDI = 3. Temporal effects of the WNS fungus were not observed for WDI because maximums were achieved in 2012, prior to the arrival of the fungus to Mammoth Cave National Park (Table 2). Evidence of lesions in wing membranes using UV light scans demonstrated positive scans for 8.2% of all bats sampled, with positive scans exceeding 20% of bats sampled in 2013 and 2014, following introduction of the WNS fungus. Two bats with positive scans in 2011 were submitted for testing and both were negative for the *Pseudogymnoascus* fungus.

Examination of the within-species variation in right forearm length indicated that sufficient variation existed in skeletal structure to support use of BMI as a measure for evaluating body condition in bats (Table 1). In general, the heavier the species the larger the mean BMI value, with big brown bat *Eptesicus fuscus* exhibiting the largest and eastern small-footed bat *Myotis leibii* the smallest mean BMI. Yearly variation in BMI was observed for little brown bats ($F = 6.36$, $P = 0.0008$) and northern long-eared bats ($F = 3.34$, $P = 0.0192$), but not Indiana bats ($F = 0.94$, $P = 0.4283$) or tri-colored bats ($F = 1.88$, $P = 0.131$; Figure 2). Mean BMI for little brown bats and northern long-eared bats was greater in 2014 than previous years. Patterns for mean body mass showed significant yearly variation only for little brown bats ($F = 4.02$, $P = 0.0112$), despite an apparent increase in body

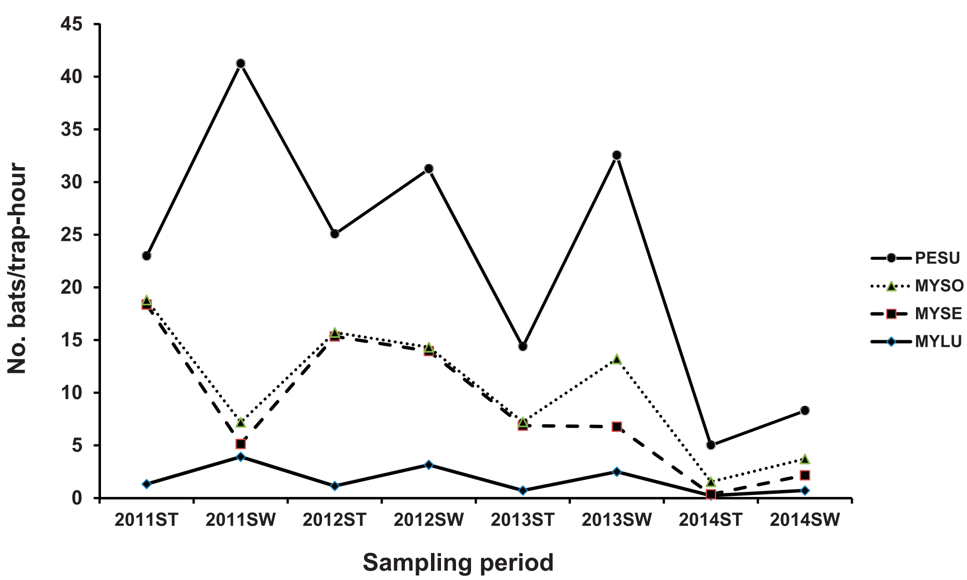

Figure 1. Capture rates (bats/trap-hour) for four species of bats at Colossal Cave, Mammoth Cave National Park, Kentucky, during harp trapping in spring staging (ST) and autumn swarming (SW) from 2011 to 2014. Species abbreviations are as follows: MYLU (little brown bat, *Myotis lucifugus*), MYSE (northern long-eared bat, *M. septentrionalis*), MYSO (Indiana bat, *M. sodalis*), and PESU (tri-colored bat, *Perimyotis subflavus*).

Table 2. Yearly percentages of wing damage (WDI: 0–3)[a] and presence of fungal spores (UV Scan: positive [POS] vs. negative [NEG]) across all species of bats captured[b] at Colossal Cave, Mammoth Cave National Park, Kentucky, 2011 to 2014.

	2011	2012	2013	2014
WDI (*n*)	328	374	302	134
0	94.5	82.9	91.7	91.8
1	5.5	16.6	8.3	7.5
2	—	0.5	—	0.7
UV Scan (*n*)	163	374	175	94
POS	1.2	—	23.4	24.5
NEG	98.8	100	76.6	75.5

[a] Wing damage index score follows the approach in Reichard and Kunz (2009).
[b] Species include: tri-colored bat *Perimyotis subflavus,* northern long-eared bat *Myotis septentrionalis,* little brown bat *Myotis lucifugus,* Indiana bat *Myotis sodalis,* eastern small-footed bat *Myotis leibii,* Rafinesque's big-eared bat *Corynorhinus rafinesquii,* big brown bat *Eptesicus fuscus,* and eastern red bat *Lasiurus borealis*.

mass in 2014 for northern long-eared bats (F = 2.19, P = 0.0884; Figure 3). Regardless, little brown bats demonstrated highest mean body mass values in 2014, following exposure to the WNS fungus.

Mean BMI showed significant variation across sampling periods for little brown bats (F = 4.34, P = 0.0019), northern long-eared bats (F = 14.7, $P < 0.0001$), and tri-colored bats (F = 29.0, $P < 0.0001$), but not for Indiana bats (F = 0.99, P = 0.4283; Figure 4). In general, mean BMI was highest for most species during the third sampling period of autumn swarming (SW3 or late swarming). Patterns for body mass paralleled those for BMI, with significant variation recorded across sampling periods for little brown bats (F = 4.33, P = 0.0019), northern long-eared bats (F = 15.3, $P < 0.0001$), and tri-colored bats (F = 25.2, $P < 0.0001$), but not Indiana bats (F = 1.18, P = 0.3286; Figure 5). Tri-colored bats exhibited the greatest percent increase in body mass (42.5%) and BMI (42.9%) of any species prior to entering hibernation from minimum values observed in late staging (ST3; Figures 2–5). The sole significant interaction between year and sampling period was for BMI in northern long-eared bats (F = 4.03, $P < 0.0001$); however, an explanation for this outcome is not readily clear.

Discussion

Male-biased sex ratios predominate in bats at swarming caves during autumn (Piksa 2008; Šuba et al. 2008; Vintulis and Šuba 2010). Bats at Colossal Cave demonstrated the same pattern for all species that hibernated in the cave. Swarming behavior, such as mating or chasing, was not observed at the entrance to the cave on any night of sampling across the 4 y of survey, suggesting swarming likely occurred elsewhere in the park. Levels of wing damage due to WNS did not change over time, but the percentage of bats possessing fungal lesions increased markedly during the final 2 y of sampling, concurrent with noticeable declines in bat capture rates,

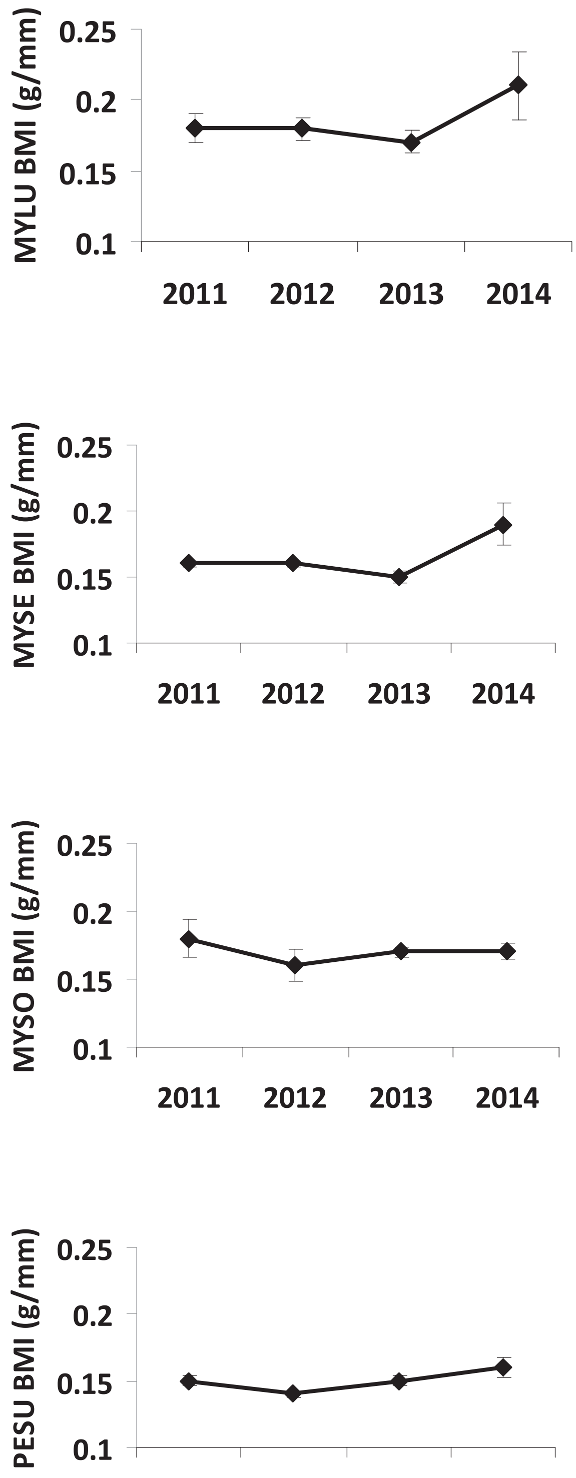

Figure 2. Mean (±2 SE) body mass index (BMI: g/mm) of bats each year of sampling, 2011 to 2014, for species captured at Colossal Cave, Mammoth Cave National Park, Kentucky. Species abbreviations are as follows: MYLU (little brown bat, *Myotis lucifugus*), MYSE (northern long-eared bat, *M. septentrionalis*), MYSO (Indiana bat, *M. sodalis*), and PESU (tri-colored bat, *Perimyotis subflavus*).

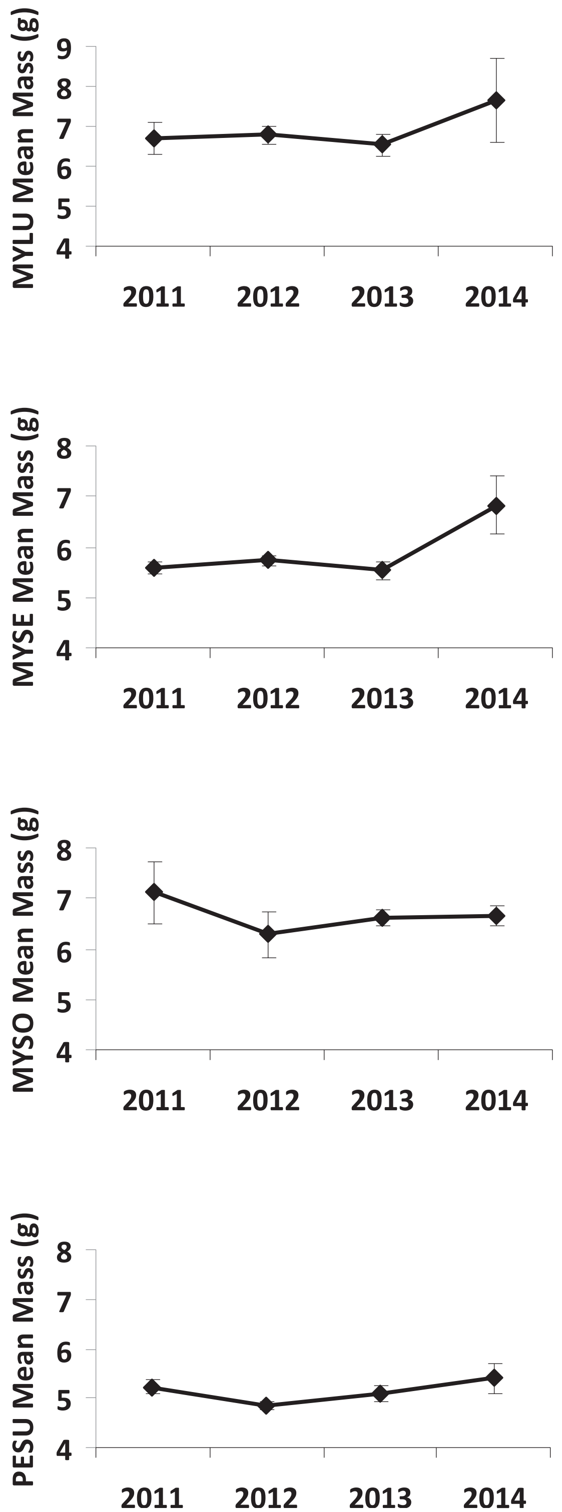

Figure 3. Mean (±2 SE) body mass (g) of bats each year of sampling, 2011 to 2014, for species captured at Colossal Cave, Mammoth Cave National Park, Kentucky. Species abbreviations are as follows: MYLU (little brown bat, *Myotis lucifugus*), MYSE (northern long-eared bat, *M. septentrionalis*), MYSO (Indiana bat, *M. sodalis*), and PESU (tri-colored bat, *Perimyotis subflavus*).

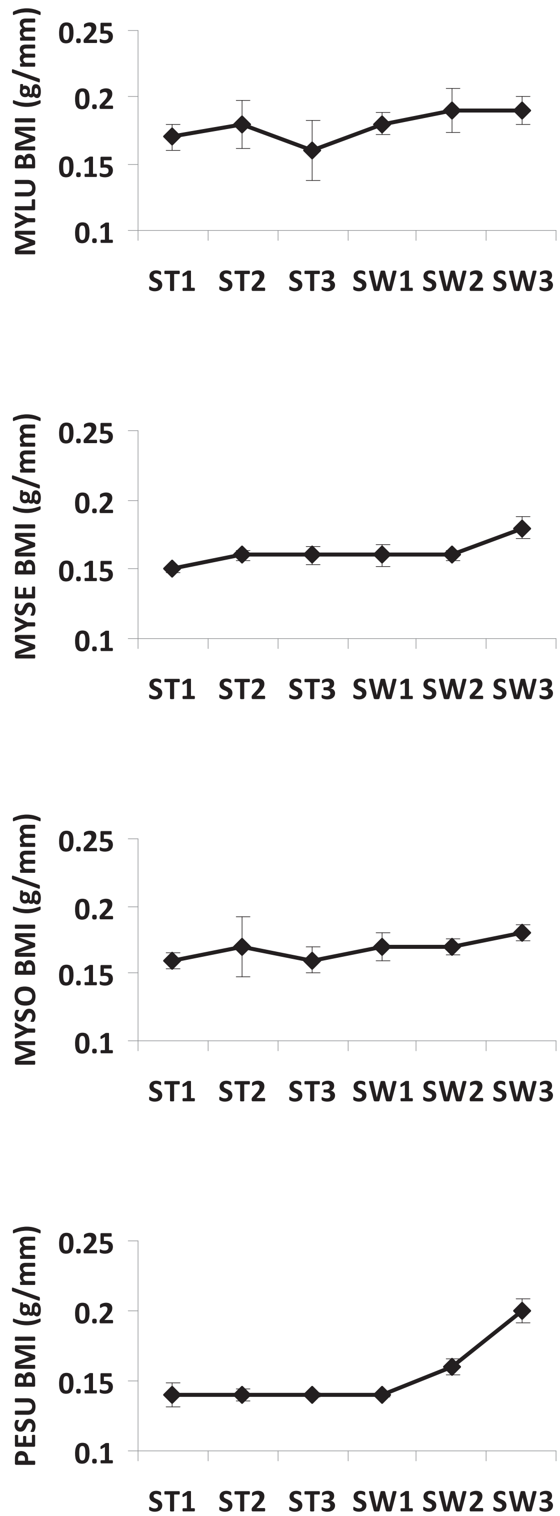

Figure 4. Mean (±2 SE) body mass index (BMI: g/mm) of bats by sampling period for species captured at Colossal Cave, Mammoth Cave National Park, Kentucky, 2011 to 2014. Species abbreviations are as follows: MYLU (little brown bat, *Myotis lucifugus*), MYSE (northern long-eared bat, *M. septentrionalis*), MYSO (Indiana bat, *M. sodalis*), and PESU (tri-colored bat, *Perimyotis subflavus*). Sampling periods are as follows: early staging (ST1), mid-staging (ST2), late staging (ST3), early swarming (SW1), mid-swarming (SW2), and late swarming (SW3).

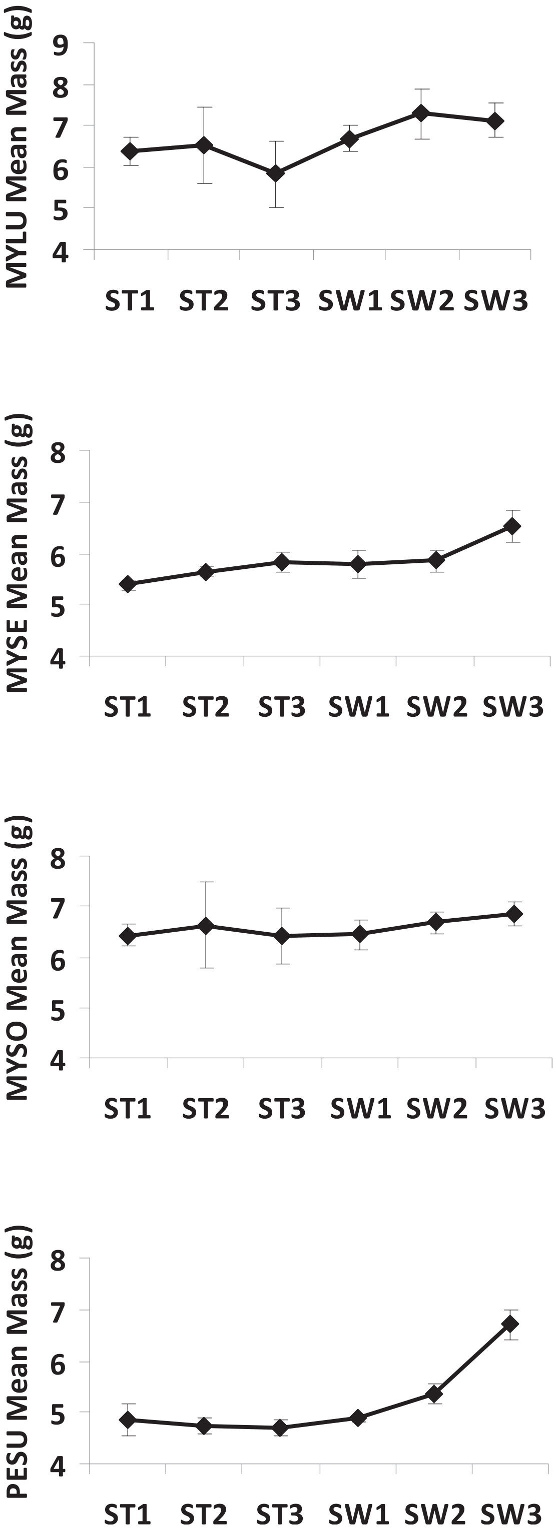

Figure 5. Mean (±2 SE) body mass (g) of bats by sampling period for species captured at Colossal Cave, Mammoth Cave National Park, Kentucky, 2011 to 2014. Species abbreviations are as follows: MYLU (little brown bat, *Myotis lucifugus*), MYSE (northern long-eared bat, *M. septentrionalis*), MYSO (Indiana bat, *M. sodalis*), and PESU (tri-colored bat, *Perimyotis subflavus*). Sampling periods are as follows: early staging (ST1), mid-staging (ST2), late staging (ST3), early swarming (SW1), mid-swarming (SW2), and late swarming (SW3).

especially in 2014. Entries into the cave by National Park Service park personnel in winter 2013 and 2014 found no mass mortalities, suggesting most bats had either abandoned the hibernaculum (perhaps in response to WNS infection) or died on the landscape. The apparent disappearance of northern long-eared bats from the cave following arrival of the WNS fungus is similar to patterns observed for this species in Arkansas upon introduction of the WNS fungus (B. Sasse, Arkansas Game and Fish Commission, personal communication).

Mean BMI varied among species, consistent with results for bats swarming at caves in Latvia (Šuba et al. 2011). Larger bats, such as big brown bat, possessing higher BMI values may have a selective advantage in responding to WNS by carrying greater fat reserves to sustain them through hibernation, regardless of the extent of exposure to the fungus. Conversely, eastern small-footed bats and tri-colored bats had mean BMI values (≤0.15) well below those reported for other species during swarming or staging (Fuller et al. 2011; Šuba et al. 2011; Lowe 2012). Therefore, these two smaller bat species may be more vulnerable to accelerated losses in body mass due to WNS infection. Tri-colored bats exhibited the greatest change (42.9%) in mean BMI and mean body mass (42.5%) from early staging to late swarming, suggesting they have a hibernation strategy that already leads to significant weight loss, even without WNS infection. This percent increase was larger than percent increases reported for body mass in little brown bats (32.9% males, 29.6% females) upon entering hibernation (Kunz et al. 1998).

Mean BMI values of little brown bats (range = 0.18–0.19) recorded during swarming in our study were lower than those reported for the species in Nova Scotia (0.22; Lowe 2012) and two New England states (>0.2 for bats with WDI ≤ 2; Fuller et al. 2011), suggesting little brown bats at the southern edge of their distribution may enter hibernation with lower fat reserves than individuals hibernating farther north. Published estimates of mean forearm length in little brown bats vary across North America, with values greater than ours in Indiana (38 mm; Whitaker et al. 2007), Pennsylvania (38.1 mm; Whitaker and Hamilton 1998), and Colorado (38.6 mm; Schorr and Navo 2012), but smaller in British Columbia (36.4 mm, Nagorsen and Brigham 1995); in Texas values were as low as 34 mm (Schmidly 1991). These data suggest that no apparent variation exists in the body structure of little brown bats by latitude that would account for the lower BMI values we recorded for individuals roosting further south. Based on the patterns observed, we offer two possible scenarios for little brown bats hibernating in southern North American cave systems: 1) lowered fat reserves lead to high mortality rates upon WNS infection as a result of exhaustion of insufficient fat stores before spring emergence (Reeder et al. 2012); or 2) lowered fat reserves accompany bats that annually experience shorter hibernation periods relative to bats hibernating farther north in latitude; thus, bats are more likely to withstand impact of WNS infection as a result of reduced length of exposure to the fungus each winter (Johnson et al. 2012). It should be noted that our sampling of bats was truncated and did not include individuals throughout October; thus, it is plausible that the maximum prehibernation mean BMI value for this species in the bats we studied was greater than reported here.

Consistent with our hypothesis, BMI was highest during late swarming, as observed in other bats during autumn (Šuba et al. 2011). Studies of male little brown bats in Nova Scotia, however, found BMI values increased in midswarming, only to decline just prior to bats entering hibernation (Lowe 2012). Regardless, the significant increases in BMI observed for little brown bats and northern long-eared bats in 2014, following a winter of exposure to the WNS fungus, suggest that individuals surviving exposure to the fungus were in better condition and likely heavier than individuals that did not survive or dispersed elsewhere. Studies on cave-hibernating bats at other hibernacula are needed to confirm this possibility.

Although bats exhibit fidelity to swarming sites (Glover and Altringham 2008), movement of bats in autumn among swarming sites is well-documented for many species in northern latitudes, with distances ranging from 5 to 21 km in Latvia (Šuba et al. 2008), 0.6 to 1.5 km in northern England (Rivers et al. 2006), and up to 31.5 km in Poland (Furmankiewicz 2008). In North America, patterns of movement among hibernacula for little brown bats can reach 500 km, with a median distance of 315 km (Norquay et al. 2013). Further, size of catchment areas associated with specific hibernacula and swarming sites can be large (Rivers et al. 2006; Glover and Altringham 2008), and varies geographically for Indiana bats in North America with larger catchment areas for hibernacula at more southerly latitudes (Britzke et al. 2012). Recent evidence indicates that migration of females across landscapes is believed to be a mechanism for bat-to-bat transmission of the WNS fungus for at least little brown bats (Miller-Butterworth et al. 2014). We suggest that movement of bats during autumn swarming is likely contributing to the spread of the WNS fungus among eastern North American bats because swarming provides an environment whereby fungal spores can be spread among individuals because of the extended intraspecific behavioral interactions that occur.

Evidence for male little brown bats during swarming in Nova Scotia shows individuals in better body condition return less frequently to sites to engage in mating behavior than do bats in poorer physiological condition (Lowe 2012), possibly reducing their exposure to the WNS fungus. This pattern demonstrates the complexity of interaction among body condition, mating success, and bat behavior in autumn swarming; this subject is in need of further study if we are to fully comprehend the impact of WNS on cave-hibernating bats in North America. We predict that bats in better physiological condition (i.e., higher BMI values) should be more capable of long-distance movements during autumn swarming, with the possibility that these bats are less affected by the WNS fungus and less likely to carry and disperse fungal spores (Fuller et al. 2011).

Supplemental Material

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Table S1. Description file (.xls) of field headings in Table S2.

Found at DOI: http://dx.doi.org/10.3996/042015-JFWM-033.S1 (241 KB XLS).

Table S2. Data file (.xls) of body condition assessments of bats captured from 2011 to 2014 at the entrance of Colossal Cave, Mammoth Cave National Park, Kentucky.

Found at DOI: http://dx.doi.org/10.3996/042015-JFWM-033.S1 (241 KB XLS).

Table S3. Description file (.xls) of URL or ISBN for supplemental references.

Found at DOI: http://dx.doi.org/10.3996/042015-JFWM-033.S2 (9 KB XLSX).

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Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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