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Population-level impact of white-nose syndrome on the endangered Indiana bat

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Establishing status and trend for an endangered species is critical to recovery, especially when it is faced with a nascent extinction agent. We calculated, with hierarchical log-linear change-point models, hibernaculum-level population trends between 1983 and 2009 for the endangered Indiana bat (*Myotis sodalis*) now subjected to the fast-spreading fungal disease white-nose syndrome. We combined trends from 222 wintering populations before and after onset of the disease to determine trend for clusters of interacting wintering populations, recovery units, and the species. Before onset of the disease, a west-to-east gradient in trends existed, with westernmost populations declining and easternmost populations increasing in abundance. The species as a whole, however, was stationary between 1983 and 2005 (–0.5% mean annual change; 95% confidence interval [*CI*] = –2.8, +1.8%). Estimated mean population size in 2009 was 377,124 bats (195,398–957,348), with large variance apparently caused by white-nose syndrome. With the onset of white-nose syndrome (2006–2009), the species exhibited a 10.3% annual decline (95% *CI* = –21.1, +2.0%). White-nose syndrome is having an appreciable influence on the status and trends of Indiana bat populations, stalling and in some cases reversing population gains made in recent years.

Key words: change-point analysis, endangered species, *Geomyces destructans*, *Myotis sodalis*, trend estimation

White-nose syndrome has been associated with severe and abrupt declines in bat abundance in eastern North America since the winter of 2006 (Blehert et al. 2009; Frick et al. 2010a; Turner et al. 2011), spreading throughout the eastern United States and Canada. As of spring 2012, white-nose syndrome had been confirmed in hibernacula as far north as Ontario and Quebec, as far south as Alabama, and as far west as eastern Missouri; the fungus causing white-nose syndrome, *Geomyces destructans*, has been observed over a wider range, occurring in Oklahoma, for instance (Blehert et al. 2011; Foley et al. 2011). *G. destructans* has afflicted 6 species of hibernating bats (Blehert et al. 2011; Foley et al. 2011), including the little brown (*Myotis lucifugus*), northern long-eared (*M. septentrionalis*), eastern small-footed myotis (*M. leibii*), big brown (*Eptesicus fuscus*), tricolored (*Perimyotis subflavus*), and Indiana bats (*M. sodalis*). The Indiana bat is a species for which there is particular concern because of its status as endangered under the United States Endangered Species Act of 1973. The Indiana bat is also a red-listed species according to the International Union for the Conservation of Nature (Arroyo-Cabrales and Ticul Alvarez Castaneda 2008). Information regarding the spatial and temporal patterns in species abundance is needed, but not available, for predicting population-level impacts of this disease.

Indiana bats aggregate in winter in subterranean colonies; thus, the most common means for determining population size is periodic direct observation and counting of hibernating individuals in caves and mines (Hayes et al. 2009). Trained surveyors search all sections of a hibernaculum to count and identify to species all bats observed. The fidelity by bats to subterranean roosts allows researchers to focus monitoring on a few discrete locations in winter (Hayes et al. 2009).

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Historically, surveys were limited to one per year at each hibernaculum because repeated or prolonged disruption of bats during hibernation can cause increased energy expenditure from arousal and premature depletion of fat reserves (Speakman et al. 1991; Thomas 1995; Thomas et al. 1990).

Indiana bats have been counted at various times and locations since 1929; these early counts were infrequent and prospective in nature. By the mid-20th century, a number of known aggregations of Indiana bats began to be counted on a semiregular basis (Clawson 2002). By 1983, survey methods were largely standardized and all known large aggregations of Indiana bats were regularly estimated by state and federal biologists and academic chiropterologists. Many smaller and moderately sized aggregations, however, continued to be counted less frequently; the most common rotation was surveys conducted biennially (Clawson 2002; Kunz 2003). For populations that exhibit complete fidelity to a hibernaculum, this biennial count would pose no analytical problems, nor would problems occur if the counts were synchronized. However, Hayes et al. (2009:117) noted "Tallies based on direct counts involve a suite of assumptions that are rarely articulated, yet can ultimately impact their utility for inferring population trends... [A]ttempts to infer population trends... are based on the assumptions that availability and quality of roosts are static and that bats exhibit high rates of fidelity to roosts through time." *Myotis*, however, are not entirely faithful to their hibernaculum from one year to the next (Elder and Gunier 1978; Fath 2002), nor are all counts made synchronously. As a consequence, bats counted in 1 year in 1 hibernaculum may move to another nearby hibernaculum the subsequent year and be counted again. This lack of independence, if it were not accounted for, could lead to a biased estimate of the number of bats in a region as well as exert uncertain and potentially misleading effects on estimated trends and variation in trends.

A credible estimate of species population trajectory and accompanying levels of confidence are not possible absent a robust consideration of the dependency among wintering populations and the asynchronous nature of surveys. Our objectives were, therefore, manifold. First, we determined estimates of population trend for each sufficiently surveyed hibernaculum across the species range (Fig. 1). Second, with these trend estimates as the basis for inference, we hierarchically aggregated population trajectories across complexes of interacting populations, United States Fish and Wildlife Service recovery units, and the species, as a means of dampening the unknown extent of site infidelity and uncertain hibernaculum availability and quality. We accommodated many of the uncertainties and difficulties associated with these data with hierarchical Bayesian methods. Third, we tested whether the epizootic white-nose syndrome was evident within the time series of counts we analyzed. Conventional estimates of trend are insufficient for analyzing periods in which substantial shifts in mean population size and trend are expected to occur at some intervening date. Thus, our modeling

approach allowed for an estimation of trend before and after the advent of this disease.

METHODS

Hibernaculum counts.—The Indiana Bat Recovery Team maintains a database of hibernaculum data for all known (i.e., current and historic) wintering locations of Indiana bats (curated by A. King; Appendix I). This database contains detailed historical counts from hibernacula with 1 or more Indiana bat winter occurrence records. Since 2005, a biennial data request for winter population counts of Indiana bats has been sent to bat biologists across all 27 states of the species range; these data are then used in calculating a range-wide population estimate once every 2 years.

Standardization of hibernaculum surveys occurred by ~1980, so we limited our analyses of trends to those counts collected between 1983 and 2009 (the 2011 biennial survey of results was ongoing as of this analysis). Details of survey protocol are described by Kunz (2003) and Hayes et al. (2009). A mean of 103 Indiana bat hibernacula were surveyed each year (range = 39–181) across 24 states between 1983 and 2009; as Clawson (2002) noted, surveys were more commonly conducted in odd years (128 hibernacula [95% confidence interval {CI} = 109,146] in odd years versus 77 hibernacula [67, 86] in even years). Hibernaculum counts were conducted by 1–7 surveyors between January and March, typically within a 2.2-hour period (maximum = 7 hours). Approximately 12% of surveys required vertical caving gear for access to the hibernaculum. Surveyors reported that 86% of hibernaculum counts were derived by individual counting of bats; the remaining 14% of estimates were determined by multiplying the areal estimate of a cluster of hibernating bats by a bat packing density, an expansion factor determined by the surveyors. No animals were handled in the course of this study.

Trend estimation.—We used change-point modeling to estimate trend before and after the intervention of white-nose syndrome (Toms and Lesperance 2003). Change-point models can be formulated either sequentially or retrospectively; with the former, a decision is made regarding the occurrence of a change on the basis of the data, whereas in the latter, the time series of data is examined to determine if a change point has occurred in the sequence and, if so, where this change occurred. In the case of Indiana bat populations subject to white-nose syndrome, this change point is expected to evolve spatially with the spread of the disease (W. E. Thogmartin et al., in litt.). Rather than model an evolving spatiotemporal process given incomplete survey data, we took the former route to change-point modeling and set a priori a change point equivalent to year 2005. This is the year before the first recorded occurrence of *G. destructans* (Blehert et al. 2009).

We modeled the trend for each hibernaculum with the response as log(count+1) and explanatory variables as years (within the range of 1983–2009), and a constructed variable named yr0609. Yr0609 took on the value of 0 for years between 1983 and 2005, and then the value for year-2005 for
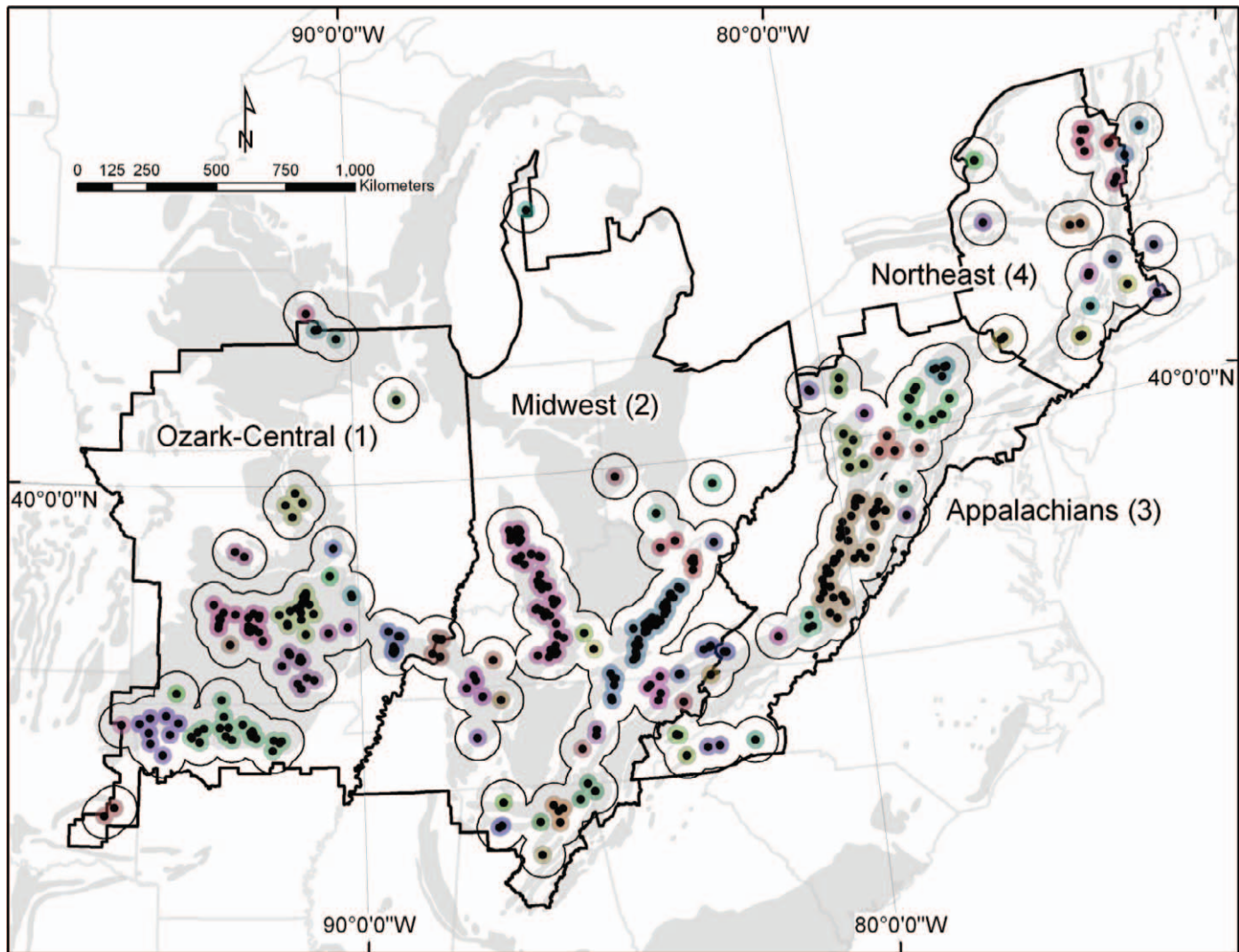
Fig. 1.—Historical hibernacula (in black) of Indiana bats in the United States, primarily associated with karst formations (gray), plotted by recovery unit and color-coded to reflect aggregations (or complexes) of hibernacula within 10-mile proximity. An additional buffer extends 25 miles around each hibernaculum alluding to further potential connectedness of hibernacula.

years 2005 to 2009. This creates an inflection point at 2005, where the fitted line was allowed to change slope. The estimated coefficient corresponding to yr0609 is the estimated change in the baseline trend estimated from 1983 to 2005. Because the yr0609 estimate is relative to the 1983–2005 trend estimate, if the 1983–2005 trend estimate is greater than the yr0609 coefficient, the coefficient for yr0609 will be negative even if the population is increasing. Conversely, if the population from 2005–2009 is estimated to be decreasing, but decreasing at a slower rate than 1983–2005, the coefficient for yr0609 will be positive. Thus, the actual trend for 2005–2009 is the sum of the 1983–2005 trend and the coefficient yr0609 for the period 2005–2009.

The linear trend for each hibernaculum was estimated with WinBUGS 1.4 (Lunn et al. 2000) using R2WinBUGS (Sturtz et al. 2005) in the R statistical language (R Development Core Team 2010). WinBUGS is a statistical package conducting Bayesian inference with Markov chain Monte Carlo methods

(Gibbs sampling; Link et al. 2002; Ntzoufras 2009). We modeled with noninformative, or flat, priors (Link and Barker 2010). The coefficient parameters were given diffuse (essentially flat) normal distributions with mean of 1 and variance equal to 1,000. The precision on error was gamma distributed with shape and scale equal to 0.1. For each model, we ran three chains for 60,000 iterations, discarding the first 40,000 iterations as burn-in and thinning by 5 to reduce serial correlation (Link et al. 2002, Lunn et al. 2000). We used the Gelman–Rubin convergence diagnostic to identify whether the chains had converged for each of the main model parameters (Ntzoufras 2009).

Of 462 hibernacula, 222 had estimable coefficients with standard errors for year and yr0609. Trends were inestimable when either the hibernaculum was no longer occupied in winter ($n = 106$) or had too few surveys to calculate model coefficients ($n = 116$); of wintering populations with inestimable trends, sums of counts from 1983–2009 averaged 178 bats (some of

the larger hibernacula were not revisited or were only recently discovered). It was the 222 hibernaculum-level estimates that were then used for the aggregations of trend at complex, recovery unit, and species level. If a hibernaculum did not have an estimable regression with standard errors, it had zero weight in aggregated estimates irrespective of the historically observed number of bats.

We defined complexes of hibernacula as a means of mitigating influences of interhibernaculum movement on trend estimation. This interhibernaculum movement (immigration/ emigration) can yield rates of population change for individual wintering populations that are outside of that expected from a closed population (W. E. Thogmartin et al., in litt). A complex was defined as a collection of hibernacula within a 10-mile buffer of any other historical hibernaculum, irrespective of whether it was in present-day use. This distance was ad hoc but for our purposes yielded sensible rates of change (i.e., $\lambda \ll 2$).

The nonzero weights for each hibernaculum were calculated within each complex by dividing each hibernaculum mean population size by the total mean population size within that complex. Four time periods were investigated for their effect on these weights: 1983–2002, 1983–2009, 1997–2005, and 2006–2009. There were no appreciable differences in weights regardless of time period used, so the period 1983–2005 was used because it represents a baseline (prewhite–nose syndrome) mean condition.

Once weights were calculated, coefficients for the intercept, year, and yr0609 were combined as a weighted mean by complex level. Coefficients were assumed to be uncorrelated normal random variables with the standard error reported in the lm summary in R. Aggregated parameter means were then the sum of weights times each parameter estimate, and aggregated parameter variances were calculated by summing squares of the standard error multiplied by squares of the weights. Standard errors of aggregated parameters were square roots of these variances.

In our analysis, we assumed that there exists within each hibernaculum a linear relationship between year and log(count+1) with normal random error, with an inflection point at 2005. The linear relationship assumption within hibernaculum was checked by visual inspection, and was deemed reasonable for most hibernacula. Although resulting trend estimates are a useful first approximation, it should be noted that temporal correlation of the counts was ignored. It is likely, therefore, that standard error estimates are too small.

Another assumption is that hibernaculum counts were observed from a closed population, even though we know this is not true since bats are known to occasionally change hibernacula. We assessed the consequence of this assumption by removing demographically impossible counts and reanalyzing trend with these data points removed (<2% of all counts). We found a negligible influence on higher-level estimates of trend resulting from extreme fluctuations in counts caused by immigration, primarily because these changes generally affect only the smallest wintering populations.

Model coefficients are not straightforward in their interpretation given their logarithmic nature. Thus, we expressed estimates of population trend as percent annual change (with 95% CIs), where percent annual change = (exp[year coefficient from log-linear regression] − 1) × 100%.

RESULTS

Hibernacula.—Wintering populations in the Ozark-Central Recovery Unit before white-nose syndrome exhibited a median decline of 9% (95% $CI = -4, -13\%$) between 1983 and 2005. Conversely, wintering populations in Appalachian (+8% [3, 14%]) and Northeastern (+16% [3, 30%]) Recovery Units increased. Wintering populations in the core of the species range, the Midwest Recovery Unit, exhibited no credible change (+0.5% [−1, +3%]). This pattern in population trends suggested a west-to-east gradient (Fig. 2). This increasing trend from west to east was more obvious when wintering populations were combined via a population-weighted average to the complex level (Fig. 2), with trends in each recovery unit credibly different from its neighboring unit except for Appalachian and Northeast units (Table 1).

With the onset of white-nose syndrome (2006–2009), the species exhibited a 10.3% median annual decline from the earlier rate of change (95% $CI = -21.1, +2.0\%$). However, it is not certain that this annual decline after 2005 can be explained wholly by white-nose syndrome at our level of examination, as spatial patterns in trends indicated considerable declines in abundance not apparently associated with the occurrence of this disease (e.g., in Tyson Quarry, St. Louis County, Missouri; Fig. 3). There were increasing populations of hibernating Indiana bats in white-nose syndrome-affected counties, as well (i.e., Skinner Hollow, Bennington County, Vermont, and Bellamy, Montgomery County, Tennessee).

For the 16 largest hibernacula, comprising more than 80% of the estimated population, 10 of 16 exhibited a reduction in the hibernating population since 2006, even in areas where white-nose syndrome was absent (Appendix II). The largest hibernaculum, Twin Domes in Harrison, Indiana, began with ~83,000 hibernating bats and declined to ~49,000 hibernating bats by 2005, and thereafter declined precipitously to ~17,000 hibernating bats by 2009. Conversely, Ray's Cave in Greene, Indiana, the 2nd-largest hibernaculum, increased from ~17,000 to ~72,000 between 1983 and 2005, and then began to decline (this decline may have begun as early as 1998), with a current population somewhere on the order of 54,000 hibernating bats. Wyandotte Cave in Crawford, Indiana also experienced a great increase in abundance, increasing from ~5,000 to ~52,000 hibernating bats; after 2005 the increase ameliorated with a 2009 population on the order of ~46,000 bats.

Recovery unit.—Recovery considerations for the Indiana bat under the Endangered Species Act are determined for populations within recovery units. The Midwest Recovery Unit possessed the largest population over the interval 1983– 2009 (Fig. 4); although the median population estimates over
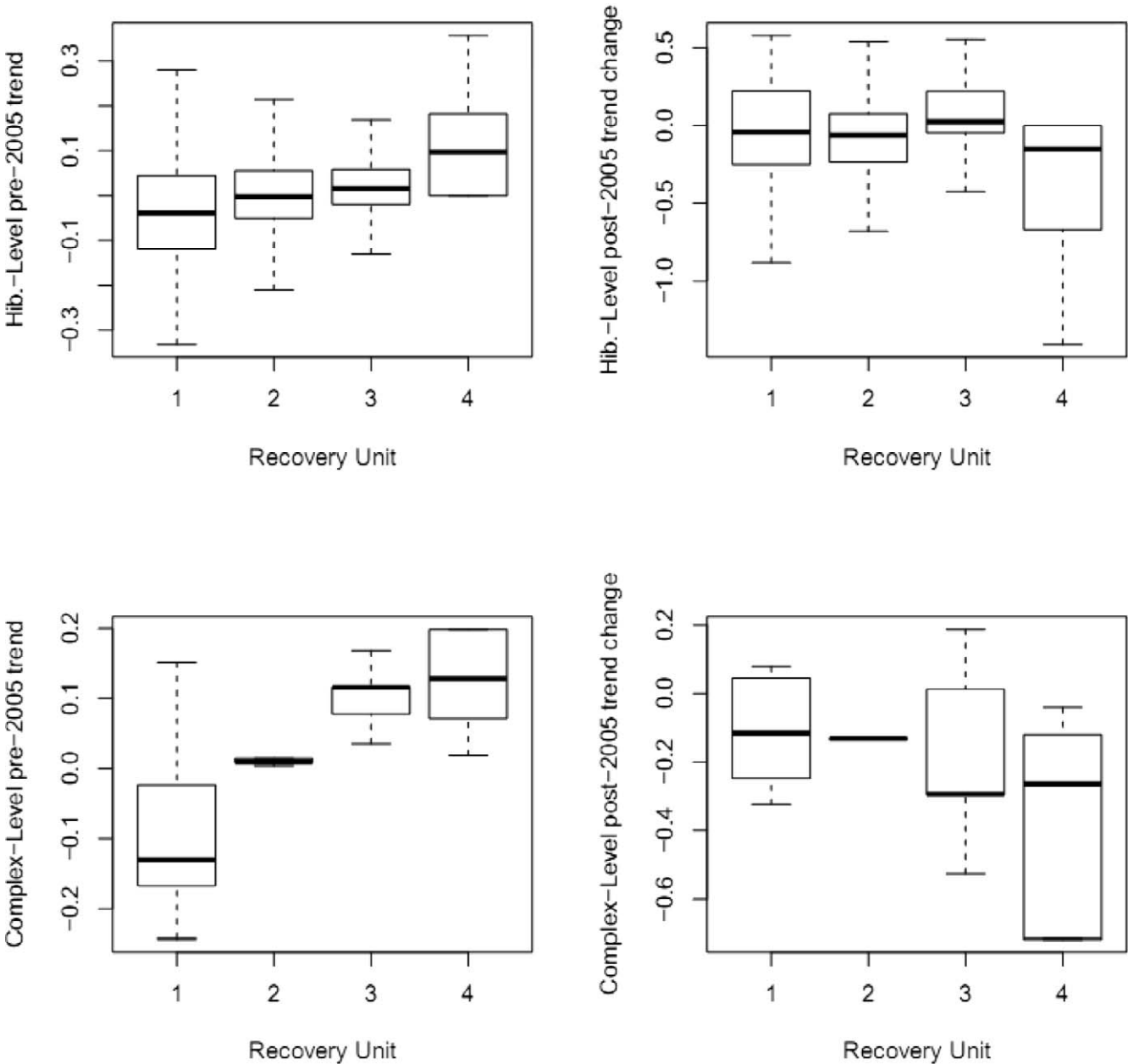
Fig. 2.—Mean (95% confidence interval) hibernacula and complex trend and changes in trend estimates plotted by recovery unit. Note differing ordinate. Recovery units are Ozark-Central (1), Midwest (2), Appalachian (3), and Northeast (4).

Table 1.—Mean parameter estimates (intercept, 1983–2003 trend, and 2003–2009 trend) for hibernacula, complex, and recovery unit levels (with 95% confidence intervals). *n* is the number of hibernacula per recovery unit contributing to the hibernacula trend estimates.

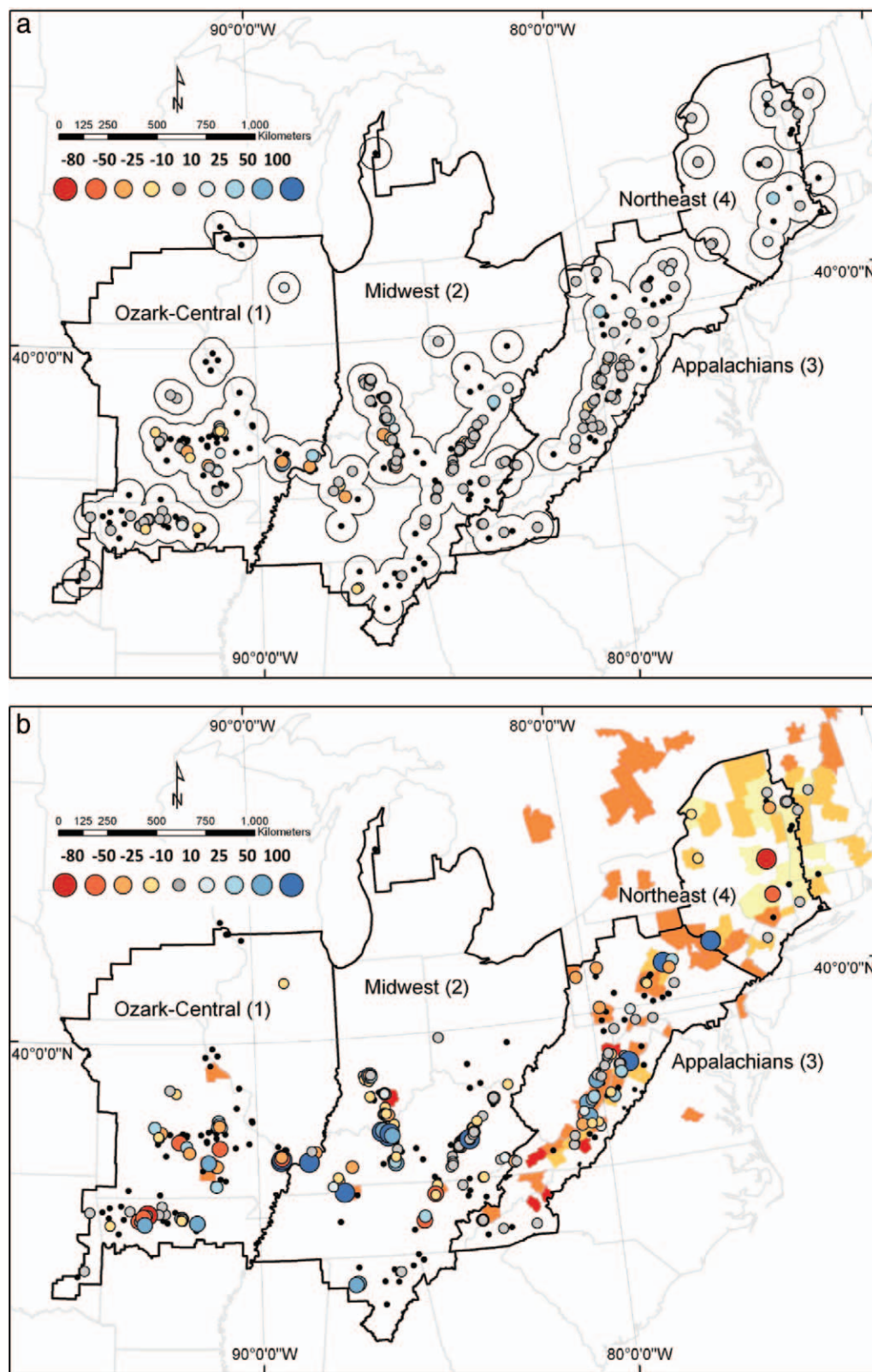| Recovery unit (n)	Hibernacula			Complex			Recovery unit		
	Intercept	1983–2005	2006–2009	Intercept	1983–2005	2005–2009	Intercept	1983–2005	2005–2009
1 (57)	4.65	−0.06	−0.11	7.29	−0.06	−0.11	9.15	−0.09	−0.06
	(−0.56, 11.81)	(−0.47, 0.27)	(−1.29, 0.99)	(0.88, 11.10)	(−0.24, 0.28)	(−0.32, 0.08)	(8.26, 10.04)	(−0.14, −0.04)	(−0.35, 0.23)
2 (101)	4.74	−0.0004	0.01	7.59	0.002	−0.02	9.65	0.01	−0.09
	(−0.76, 9.91)	(−0.26, 0.26)	(−0.84, 1.15)	(1.51, 10.43)	(−0.19, 0.05)	(−0.37, 2.50)	(9.39, 9.91)	(−0.01, 0.03)	(−0.21, 0.03)
3 (49)	2.25	0.02	0.07	5.20	0.10	−0.20	6.73	0.08	−0.15
	(−0.40, 6.63)	(−0.12, 0.16)	(−0.59, 0.70)	(−1.29, 7.96)	(−0.03, 0.18)	(−0.53, 0.19)	(5.86, 7.59)	(0.03, 0.13)	(−0.70, 0.40)
4 (14)	2.70	0.11	−0.46	4.59	0.13	−0.52	5.92	0.15	−0.53
	(−1.41, 7.56)	(−0.0003, 0.31)	(−1.85, 0.001)	(−1.79, 7.50)	(0.02, 0.20)	(−2.06, −0.04)	(3.62, 8.22)	(0.03, 0.27)	(−0.93, −0.13)

FIG. 3.—Hibernacula trends pre- and postonset of white-nose syndrome. Larger-sized bubbles denote greater trend magnitude; warmer colors denote negative trends; cooler colors denote positive trends. Scale is equivalent in both panels. White-nose syndrome-affected counties are shown in light red with postonset hibernacula trend estimates.
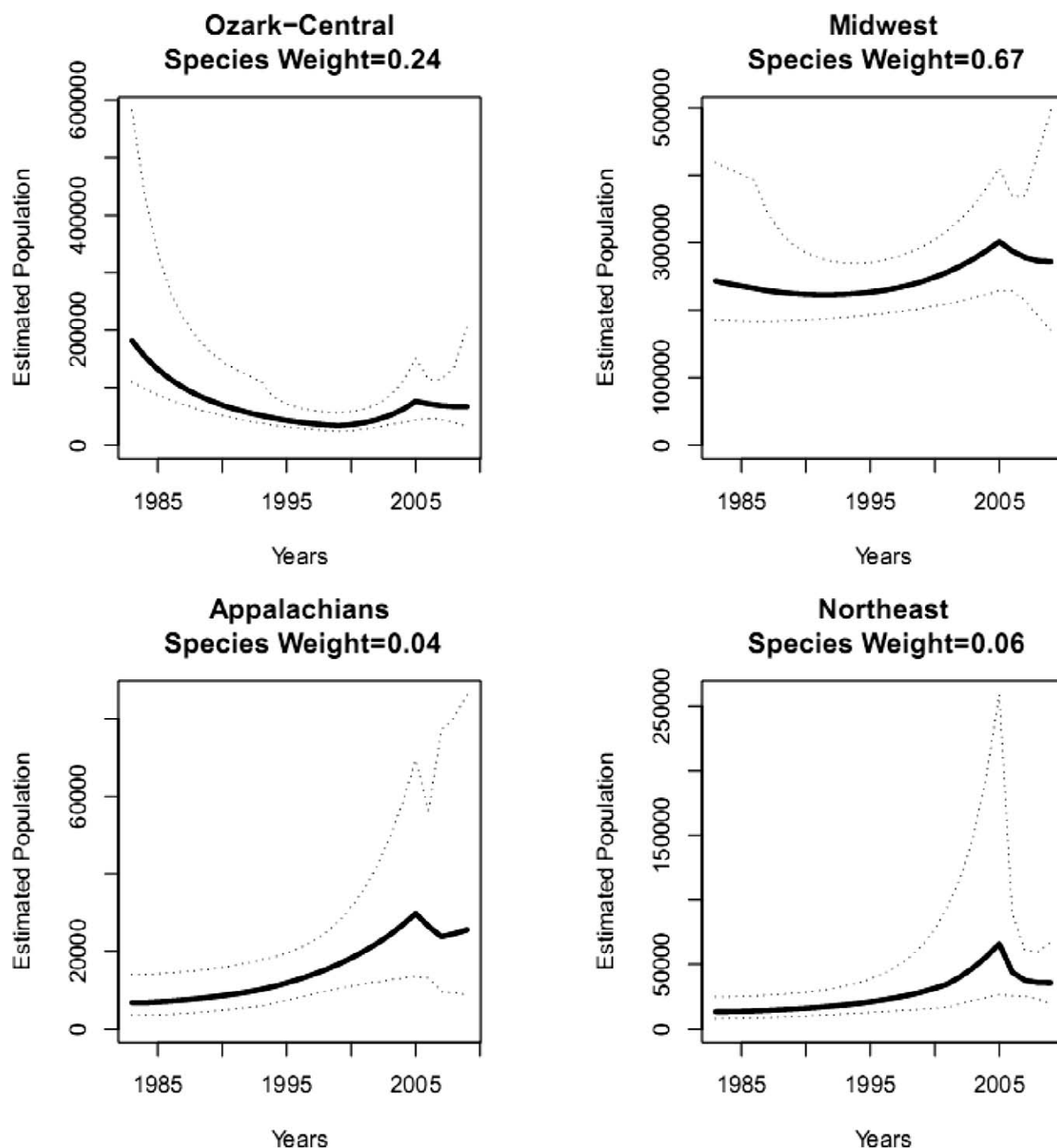
Fig. 4.—Patterns in estimated annual population size of Indiana bats in four recovery units (with 90% *CI*s). Species weights describe proportional weight of each recovery unit to the total species-level population size estimate.

the interval suggested an increase of ∼29,000 bats (+12%), the wide confidence intervals around the estimates precluded definitive statements about population increase. This was not the case for the Appalachian Recovery Unit, which increased a credible 276%, increasing from ∼7,000 to ∼26,000 bats. Conversely, the Ozark-Central Recovery Unit declined 81% between 1983 and 1999, from 182,000 bats down to ∼34,000 bats, but then rebounded by 130% from the 1999 population,

increasing by ∼33,000 bats; the overall decline for the period was 63%. The Northeast Recovery Unit grew 395% between 1983 and 2005 (from 13,000 bats to 66,000 bats), but then declined thereafter by 46% (2009 population estimate of 36,000 bats).

A significant portion of the decline after 2002 for the Northeast Recovery Unit appears to be due to white-nose syndrome (Fig. 5). Particularly hard hit were Walter Williams
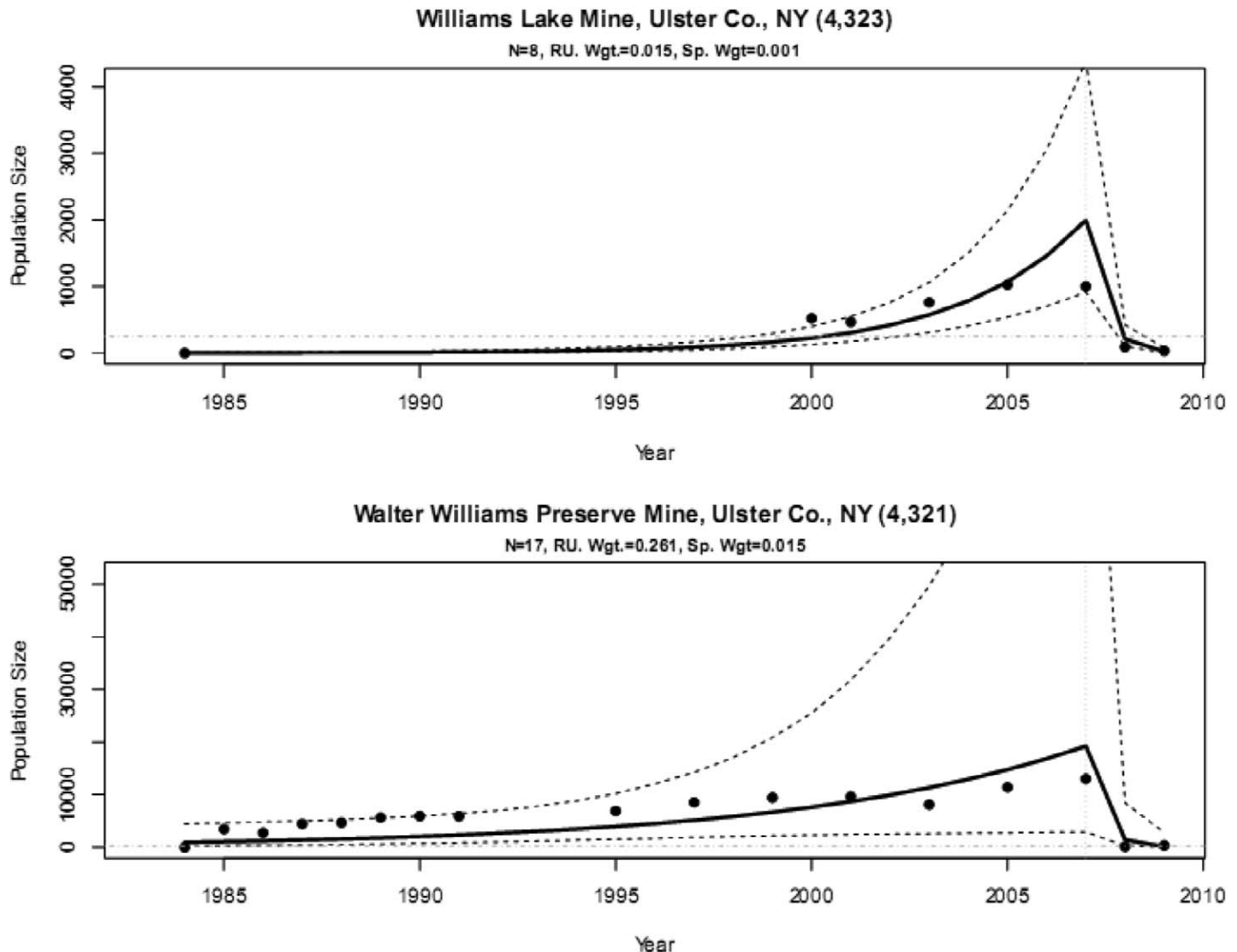
FIG. 5.—Patterns in population change (with 95% confidence intervals) for 2 hibernacula complexes known to be affected by white-nose syndrome; the change point in these particular models were fit to the year of known infection as opposed to year 2005.

Preserve Mine (possessing 26.1% of the recovery unit population) and Williams Lake Mine (1.5%) in a 5-hibernaculum complex in Ulster County, New York, a complex comprising approximately 67% of the Northeast Recovery Unit population. These populations declined by 90% (95% $CI = 78$–97%) and 84% (22–99%), respectively. Infection in a 55-hibernaculum complex in a 12-county area of Virginia and West Virginia also appears to have stalled a growing population in the Appalachian Recovery Unit.

Species.—The species exhibited a nonsignificant 0.5% annual decrease (95% $CI = -2.8, +1.8\%$) between 1983 and 2005 (Fig. 6). On the basis of years for which we had the most survey information, 2004–2006, we predicted annual species population sizes of 432,720 (278,026–907,156), 473,537 (285,375–1,130,074), and 429,573 (292,339–712,898) hibernating Indiana bats, respectively (Table 2). In 2005, 1983, and 2009, estimates were the 1st, 2nd, and 7th highest median population sizes, respectively, for the period. The mean

probability of the species exceeding the recovery criteria population size of 457,000 bats in any year was 20.5%.

DISCUSSION

The range-wide population of Indiana bat appears to have been in a stationary state for at least 2 decades before the onset of white-nose syndrome. White-nose syndrome has caused regional decline of Indiana bats in the northeastern United States, and halted a population increase in the Appalachians, but the species-wide population size has not credibly declined. Thus, as of 2009, the disease does not appear to be sufficiently prevalent across the core portion of the species range to alter species status.

Even in the Northeast Recovery Unit where the species was first and most afflicted by white-nose syndrome, some wintering populations experienced increases in abundance. There are at least two possible reasons for this increase. Indiana bats may have continued the prewhite-nose syndrome pattern
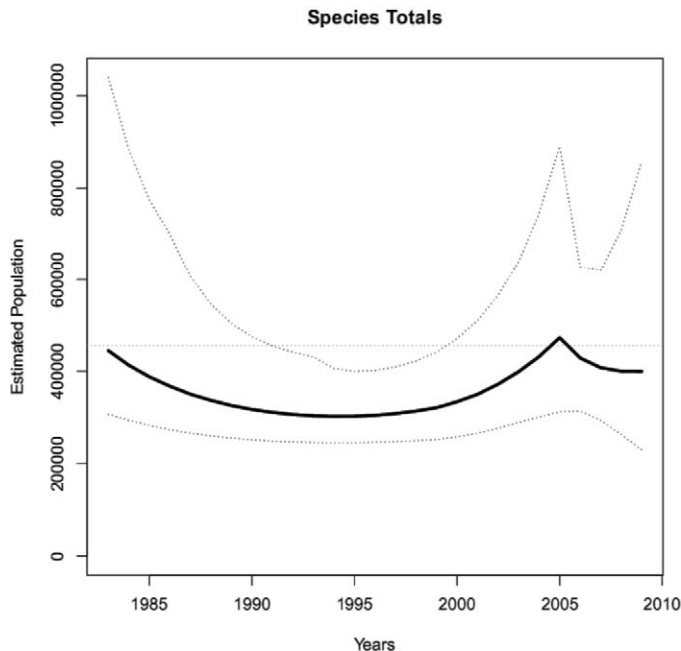
Species Totals

FIG. 6.—Predicted patterns in total annual population size of Indiana bats between 1983 and 2009 (with 90% *CI*). The dashed horizontal line is the recovery criteria for this species, 457,000 bats.

TABLE 2.—Annual estimated population size for Indiana bats between 1983 and 2009.

Year	Mean	2.5% confidence level	97.5% confidence level
1983	368,547	247,350	1,022,807
1984	339,960	237,329	778,866
1985	322,553	232,567	630,927
1986	307,881	226,033	856,380
1987	299,935	225,479	654,191
1988	292,417	224,234	540,295
1989	281,720	220,235	457,614
1990	273,771	217,662	409,226
1991	267,804	215,780	376,652
1992	263,391	214,376	381,704
1993	268,375	217,358	463,292
1994	266,990	217,288	385,867
1995	268,175	217,604	364,950
1996	279,927	224,112	388,422
1997	283,794	225,260	393,182
1998	290,654	227,581	410,188
1999	309,988	235,412	459,961
2000	324,143	240,666	504,157
2001	349,323	250,627	575,879
2002	372,195	259,819	649,742
2003	399,172	269,591	752,208
2004	432,720	278,026	907,156
2005	473,537	285,375	1,130,074
2006	429,573	292,339	712,898
2007	407,026	271,965	709,385
2008	383,207	233,865	808,103
2009	377,124	195,398	957,348

of increase in areas unaffected by disease. Alternatively, bats aroused from hibernation have been recorded switching hibernacula in the midst of winter likely in response to disturbance (Elder and Gunier 1978). The increases we observed in wintering populations in the Northeast Recovery Unit may be the mass movement of individuals to as-yet-unaffected hibernacula. Unfortunately, the lack of information on interhibernacula movement in *Myotis* species, let alone Indiana bats, precludes us from distinguishing between these hypotheses.

There was some evidence of a west-to-east gradient in population trends, possibly indicating a north and eastward movement in species range during the period of our observations. An increasing number of species are exhibiting shifts in range, often in association with changes in climate (Parmesan et al. 1999; Parmesan and Yohe 2003; Root et al. 2003; Walther et al. 2001, 2002). Both Frick et al. (2010b) and Adams (2010) indicated that higher precipitation was related strongly to higher bat reproduction, with Adams (2010) suggesting that these relations may lead to distributional changes in an altered climate. Humphries et al. (2002) described how warming winters may lead to increased overwinter survival in the northern portion of bat species ranges. Increased precipitation in the eastern United States since about 1970 coupled with warming winter conditions (Hayhoe et al. 2007; Karl and Knight 1998; McCabe and Wolock 2002) may allow for higher reproduction and winter survival in the Northeast Recovery Unit. Under a regime of increasing temperature and precipitation (Hayhoe et al. 2007; Najjar et al. 2000), conditions in the northeast are expected to continue improving for bats (Robinson et al. 2005). The

decrease in the Ozark-Central Recovery Unit could be climate mediated as well, but lack of similar declines in the Midwest Recovery Unit and in southern portions of the Appalachian Recovery Unit argues against latitudinally related climate characteristics (such as temperature) and instead favors longitudinal changes in precipitation gradients as the cause for declines in the southwestern portion of the species range.

Other nonclimate-related factors, such as gating of cave entrances, altered forest conditions, or loss of habitat from urbanization, are also likely to play a role in regional gradients in trend (Jones et al. 2009; United States Fish and Wildlife Service 2007), possibly one larger than climate. For instance, reduced insect prey accompanying widespread intensification of agricultural practices is one potential culprit for declines in the Ozark-Central and Midwest Recovery Units (Boyles et al. 2011; Kunz et al. 2011; Wickramasinghe et al. 2003, 2004). Recently, renewable energy generation has resulted in the erection of thousands of wind turbines in the midwestern United States, resulting in significant mortality of both migrant and resident bats (Arnett et al. 2008; Johnson et al. 2002; Kunz et al. 2007); few Indiana bats, however, have ever been recorded dying from wind turbine collision and to our knowledge no assessment of the species-level consequences of wind generation has been conducted for Indiana bats. If spatially and temporally varying covariates were available, examining these various causal factors in the context of the hierarchical log-linear models we used would allow us to

TABLE 3.—Winter population estimates for Priority 1A ($n = 16$) and 1B ($n = 7$) Indiana bat hibernacula as described in the draft recovery plan (United States Fish and Wildlife Service 2007, table 2). All P1 hibernacula ($n = 23$) have at some point in the recorded past had ≥10,000 hibernating Indiana bats and currently provide suitable winter habitat. P1A hibernacula have maintained a minimum of 5,000 Indiana bats during the last 10 years, whereas P1B hibernacula have not met this criterion in the last 10+ years.

State	County	Hibernaculum	Priority	Maximum estimate since 1960	Recovery plan 2005 estimate	Model-based 2005 estimate
Illinois	Alexander	Magazine Mine	P1A	33,500	33,500	49,354
Indiana	Crawford	Batwing Cave	P1A	50,000	6,850	6,195
Indiana	Crawford	Wyandotte Cave	P1A	54,913	54,913	52,343
Indiana	Greene	Ray's Cave	P1A	62,464	54,325	72,442
Indiana	Harrison	Jug Hole Cave	P1A	29,430	29,430	28,918
Indiana	Harrison	Twin Domes Cave	P1A	100,000	36,800	48,585
Indiana	Monroe	Coon Cave	P1A	10,675	9,270	11,531
Indiana	Monroe	Grotto Cave	P1A	10,338	9,875	6,613
Kentucky	Carter	Bat Cave	P1A	100,000	29,500	25,039
Kentucky	Edmonson	Dixon Cave	P1A	16,550	3,100	3,206
Missouri	Iron	Pilot Knob Mine	P1A	139,000	50,550	Inestimable[a]
Missouri	Washington	Great Scott Cave	P1A	85,700	6,450	5,115
New York	Ulster	Walter Williamms Preserve Mine	P1A	11,394	11,394	28,716
New York	Ulster	Williams Hotel Mine	P1A	15,438	15,438	18,366
Tennessee	Blount	White Oak Blowhole Cave	P1A	12,500	7,861	5,965
West Virginia	Pendleton	Hellhole Cave	P1A	11,890	11,890	20,233
Kentucky	Edmonson	Coach Cave	P1B	100,000	-	8
Kentucky	Edmonson	Long Cave	P1B	7,600	1,153	622
Kentucky	Letcher	Line Fork Cave	P1B	10,000	1,844	1,314
Missouri	Crawford	Onyx Cave	P1B	12,850	180	92
Missouri	Franklin	Copper Hollow Sink Cave	P1B	21,000	250	114
Missouri	Pulaski	Brooks Cave	P1B	19,461	70	93
Missouri	Pulaski	Ryden Cave	P1B	10,539	10	3

[a] Hazardous conditions precluded safe entry into this hibernaculum, preventing winter surveys. Fall surveys at the entrance to this mine, however, suggested that large numbers of bats existed until recent years (Clawson 2002, Elliott and Kennedy 2008).

examine their potential contributions to population trends (Thomson et al. 2010).

There are a few important points to make regarding our use of change-point analyses. Variances estimated around the change point (year 2005) increased considerably relative to other years to accommodate inflections in trend. The magnitude of this variance is symptomatic of the magnitude of the change in trend between the pre- and postwhite-nose syndrome periods. Further, our log-linear regression approach ably accommodated the >80% of the population occurring in hibernacula comprised of >1,000 individuals. This approach works less well for estimating small wintering populations because of the high influence these hibernacula experience from immigration and emigration. Our hierarchical method of combining hibernaculum counts into complex, recovery unit, and species-level estimates led to a smoothing of the trend, reducing the impact of this interhibernaculum movement on the estimation process. But if the focus of trend estimation is at the scale of the hibernaculum rather than coarser scales, then methods will need to be implemented that can accommodate: the irregular nature of survey effort, especially as hibernaculum size decreases; the neighborhood context of wintering populations; potentially abundant zero or near-zero counts; and, possibly, a flexible (spatiotemporally varying) change point. Hierarchical Bayesian count models with random effects for year and the error term (to accommodate overdispersion likely to occur in the smallest populations) are a good direction

for future study (Link and Sauer 2002). A state–space formulation, which separates the observation process from the demographically determined population process, would help distinguish between environmental (process) and observational (nonprocess) sources of error (Dennis et al. 2006). Nonprocess error resulting from uncertainty in the observed counts may be reduced through incorporation of relevant covariates and smoothing of the random effect for year. Potential covariates to consider for modeling this observation process might include, for instance, survey-specific measures of observer effort, observer-generated levels of disturbance, cave complexity, air and substrate temperatures, and packing densities (Hayes et al. 2009; Tuttle 2003).

Our trend and population estimates have important implications for the federally endangered status and recovery considerations of Indiana bats. The United States Fish and Wildlife Service developed a plan to recover the species to a size sufficient for removal from the Endangered Species Act list (United States Fish and Wildlife Service 2007). We found that only in the year before the onset of white-nose syndrome (2005) did the mean estimate of Indiana bats exceed the recovery criterion of 457,000 individuals. Given our wide confidence intervals, we calculated that this criterion was exceeded with a probability of 20.5%. Our model-based results for the largest wintering populations are also quite comparable with those identified in the Recovery Plan (Table 3; United States Fish and Wildlife Service 2007, table 2), with 1

exception. We excluded an important wintering population, Pilot Knob Mine in Missouri. The Recovery Plan assumed a population size of 50,500 individuals for this hibernaculum, constituting >10% of the estimated range-wide population. We were unable to include Pilot Knob Mine in our analyses because hazardous conditions would not allow safe surveying in winter until very recently (Clawson 2002; Elliott 2008; Elliott and Kennedy 2008), resulting in too few surveys for inclusion in our estimation process. If we add 50,500 bats to each year over the period of analysis, we find that the mean estimate of Indiana bats exceeded the recovery criterion for 4 years, 2004–2007; it should be noted, however, that Elliott and Kennedy (2008) reported a much lower estimate of Indiana bats by 2008, 1,678 bats, so our model-based estimate for 2005 is likely the only year in which we can be confident that Indiana bats met the recovery goal. With the recent discovery of white-nose syndrome in the core of the species' range, subsequent population estimates are not likely to reach this recovery criterion any time soon.

ACKNOWLEDGMENTS

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Appendix I

Collation of wintering population counts of Indiana bats.—In 1995, the Indiana Bat Recovery Team requested distributional data in a letter sent to consultants, researchers, and authorities on endangered species in 28 states (Gardner and Cook 2002). From the responses received from this data request and other published and unpublished records, Gardner and Cook (2002) developed a range-wide database of county distributional records for the Indiana bat and used geographical information system (GIS) software (ArcInfo® and ArcView®, Environmental Systems Research Institute, Redlands, California) to produce seasonal distribution maps. In June 2005, the United States Fish and Wildlife Service's Bloomington Field Office e-mailed an Indiana bat hibernaculum data request to over 75 individuals, including service biologists, recovery team members, bat researchers, state and federal agency biologists, consultants, and other bat conservation partners in 27 states, who in turn forwarded the request to other colleagues. Hibernaculum data were received from all 27 states. Bloomington Field Office biologists used the combined responses from the 1995 and 2005 data requests, existing recovery team records, and other published and unpublished records (Clawson 2002, Ellison et al. 2003) to develop a GIS-based hibernaculum database containing detailed information for all known (i.e., current and historic) hibernacula with one or more Indiana bat winter occurrence records (curated by A. King). The Bloomington Field Office also requested recovery team members and service biologists from across the species' range to provide updates to summer and winter distribution maps of Gardner and Cook (2002) during an Indiana Bat Risk Assessment Workshop in March 2005 and subsequent e-mails sent after the close of the 2005 summer reproductive season. All distribution records/maps have been updated through at least October 2006 but more are added as information becomes available. Since 2005, A. King has sent out a biennial data request to bat biologists throughout the Indiana bat's range, collated resulting population data, and published a range-wide population estimate every 2 years thereafter.

APPENDIX II

Annual observed Indiana bat hibernaculum counts between 1983 and 2009, with the fitted change-point regression lines (and 95% confidence intervals [*CI*]). Hibernaculum name, county, state, and numeric identifiers are provided; the numeric identifiers identify recovery unit (1 = Ozark-Central, 2 = Midwest, 3 = Appalachian, and 4 = Northeast) and hibernaculum. Sample size (*n* surveys), recovery unit population weight, and species-level population weight are also provided. Weight is the contribution of the hibernaculum count to the total annual estimated population size of Indiana bats between 1983 and 2003. Only hibernacula with populations averaging >400 bats are shown. A quasi-extinction level of 250 bats is shown in some plots with a dashed horizontal line; the vertical dashed line indicates the year (2005) of the fixed change point. Figures supporting this appendix are available online.