Habitat selection by the Northern Long-eared Myotis (Myotis septentrionalis) in the Midwestern United States: Life in a shredded farmscape

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Introduction

The Northern Long-eared Myotis (*Myotis septentrionalis*) has recently been listed as a federally threatened species in the United States due to population declines from the fungal disease white-nose syndrome (USFWS 2015). *Myotis septentrionalis* seems to be particularly susceptible to the disease (Hoyt et al. 2016), and many populations of *M. septentrionalis* in white-nose syndrome (WNS) positive areas have been extirpated (Langwig et al. 2012; Frick et al. 2015). Additional mortality of *M. septentrionalis* is expected as the fungus spreads to new regions. To effectively monitor remaining populations of this species, it is important to understand their habitat preferences. While *M. septentrionalis* is considered a forest-dependent species (Caceres and Barclay 2000), few studies have examined habitat selection of this species in an agricultural landscape. We used acoustical methods to quantify bat activity and construct a habitat model of *M. septentrionalis* in an intensively farmed area in the Midwestern United States, where mortality from white-nose syndrome has not yet been observed. Our study confirms that *M. septentrionalis* prefers forest and avoids open habitats in this agricultural region. The best landscape variable for predicting activity in woodland sites was the proportion of forest coverage within a radius of 2000 meters. Our analysis indicates that bat activity increased exponentially as forest coverage increased. There is no evidence that *M. septentrionalis* preferred open areas at the edge of forest (within 5 m of forest edge), or that once in the woods, the distance to the forest edge had any impact on activity.

Abstract: Populations of the Northern Long-Eared Myotis (*Myotis septentrionalis*) have declined dramatically in recent years in eastern North America due to white-nose syndrome. Although *M. septentrionalis* was once common in parts of eastern North America, few studies have examined habitat selection of this species in an agricultural landscape. We used acoustical methods to quantify bat activity and construct a habitat model of *M. septentrionalis* in an intensively farmed area in the Midwestern United States, where mortality from white-nose syndrome has not yet been observed. Our study confirms that *M. septentrionalis* prefers forest and avoids open habitats in this agricultural region. The best landscape variable for predicting activity in woodland sites was the proportion of forest coverage within a radius of 2000 meters. Our analysis indicates that bat activity increased exponentially as forest coverage increased. There is no evidence that *M. septentrionalis* preferred open areas at the edge of forest (within 5 m of forest edge), or that once in the woods, the distance to the forest edge had any impact on activity.

Keywords: Habitat selection, acoustics, bats, bat detector, *Myotis septentrionalis*, Nebraska, Northern Long-eared Myotis, landscape, farmlands

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For this study, our main objective was to construct a model of habitat preferences to predict activity of *M. setentrionalis* in a shredded farmscape. To measure bat activity we used acoustical methods. In the model we sought to identify the best set of factors from our habitat variables to predict bat activity (Franklin 2009; Razgour et al. 2011). While we are modeling habitat preferences here,
we did not attempt to model factors that determine the distributional limits of this species in eastern Nebraska. For this reason we restricted our research sites to areas in eastern Nebraska within the known distribution of *M. septentrionalis* (White et al. 2016). Therefore, if *M. septentrionalis* is not detected, then we can assume it is not because we are beyond the distributional limits of the species. Below we outline specific hypotheses about the use of different habitats by *M. septentrionalis* in this agricultural landscape.

**Hypothesis 1**
*M. septentrionalis*, as a forest species, will avoid open fields and croplands. Patriquin and Barclay (2003) and Owen et al. (2003) reported the avoidance of open areas by *M. septentrionalis*, therefore the avoidance of open areas by this bat would not come as any surprise. However as part of testing this hypothesis we will also quantify the degree to which *M. septentrionalis* avoids open areas in Nebraska.

**Hypothesis 2**
Larger forests support higher activity and by inference greater density of *M. septentrionalis*. Some support for this hypothesis comes from Henderson et al. (2008) who found that the area of forest patches was positively related to the presence of *M. septentrionalis* in a forest-agricultural landscape.

**Hypothesis 3**
*Myotis septentrionalis* prefers open areas near forest edges. Many wildlife species prefer habitat edges (Harris 1988). It has been suggested that insects might be more abundant along edges of the forest because a wind shadow might concentrate them there (Verboom and Huitema 1997; Cryan et al. 2014). Patriquin and Barclay (2003) found higher use of edges by *Myotis lucifugus*, but lacked the sample size to draw a conclusion about *M. septentrionalis*. Jantzen and Fenton (2013) determined that all four species of bats they studied, including *M. lucifugus* and *M. septentrionalis*, were most active at the edge between forest and field. Such edge effects might indicate that highly shredded landscapes with more edges would support more *M. septentrionalis*.

**Hypothesis 4**
*Myotis septentrionalis* is repelled by forest edges and prefers more interior forest sites away from ecotones. The distinction between hypothesis 3 and 4 is subtle. In hypothesis 3 we are dealing with open areas near woods. In hypothesis 4 we are dealing only with wooded sites and asking if, once in the woods, bat activity is affected by the distance to the nearest forest-open edge. On the surface this may seem strange, once in the forest, why should it matter how far it is to the nearest edge? However, edges can alter the adjacent forest and might make them less suitable to some forest species. This concept has lead tropical ecologists to stress both habitat loss and fragmentation pattern in tropical forests (Lovejoy et al. 1986). This reverse edge effect might be particularly important in a highly shredded habitat such as the woodlands of eastern Nebraska where distances to edge of forest are routinely short. It would also supply a mechanism to understand why large forest patches support higher densities of *M. septentrionalis* (Henderson et al. 2008).

**Hypothesis 5**
Activity of *M. septentrionalis* will be higher along woodland streams as compared to woodland sites without streams. This hypothesis comes from the idea that streams offer added resources such as drinking water, perhaps higher insect abundances, perhaps more connectivity along the network of wooded habitats associated with streams, and possibly open flight ways for movement. Henderson and Broders (2008) found that *M. septentrionalis* were disproportionally using forests along streams; however, Owens et al. (2003) found *M. septentrionalis* preferred upland forest to riparian sites, thus there is currently some controversy about this issue.

**Hypothesis 6**
There are important locality differences in the activity of *M. septentrionalis*. This might be because some unmeasured covariates vary geographically (such as distance to hibernacula) leading to local differences in bat activity in eastern Nebraska.

**Materials and methods**
We used acoustical methods to measure activity of *M. septentrionalis*. This species has a low intensity call and probably can only be effectively detected within 15-20 m by our equipment (Adams et al. 2012 and our own unpublished data using acoustical arrays with *M. septentrionalis*). Some data suggest that bats with low intensity calls can be difficult to sample with acoustics (O’Farrell and Gannon 1999). On the other hand, some authors believe that acoustic sampling typically detects more species and is more effective for such work than active capture methods (Kalko et al. 1996; Murray et al. 1999; O’Farrell & Gannon 1999). More specifically, Murray et al. (1999) maintained that *M. septentrionalis* was sampled more effectively by acoustic methods; thus, we felt acoustic monitoring was an appropriate approach for our study.

There are questions about the use of acoustics for bat research (Barclay 1999, Britzke et al. 2013, Fenton 2000).
Perhaps most fundamental is the difficulty in correctly identifying bat species based on their acoustics (Lemen et al. 2015). In our work we have found that acoustics can be effective in distinguishing some species but not others. We maintain that *M. septentrionalis* can be distinguished from other species present within our study area (White et al. 2016). At the same time, based on our expertise, we would not attempt to distinguish *Eptesicus fuscus* and *Lasionycteris noctivagans*. Ultimately a judgment call has to be made to identify a call sequence whether left entirely to the internal logic of a software package algorithm or to some combination of software and human expertise.

In this study a two-step process was used to identify call sequences. First, Kaleidoscope Pro (2.2.2) was used to automatically identify call sequences (using the intermediate setting for accuracy/sensitivity). Second, all identifications of *M. septentrionalis* were verified by visual inspection based on methods described in White et al. (2016).

In the summer of 2015 from 21 May to 27 July we deployed acoustic detectors (SM2Bat+ detector and SMX-US and SMX-U1 microphones, Wildlife Acoustics) at 80 sites in eastern Nebraska (Washington, Douglas, Sarpy, and Cass counties; Fig. 2). Microphones were affixed to poles and were about 2-3 m above the surface of the ground. Bat call sequences were recorded as full-spectrum in WAC0 (lossless compression) format and later converted to wav format using Kaleidoscope Pro software (Wildlife Acoustics). Bat passes, a sequence of bat calls with a maximum duration of 7 seconds, were separated into files.

Recordings were only made on nights with mostly fair weather to avoid variation in bat activity because of stormy weather. Detectors were only left out one night at each site. The number of nights that are recorded at each site is an important question in acoustical studies. In studies using presence/absence data, the probability of detecting a species is closely tied to the number of nights surveyed (Mackenzie and Royle 2005). Few nights would be needed to sample common species but many more nights for rare species (> 45 nights, Skalak et al. 2012). Therefore when surveying for a species of bat, researchers need to conduct a cost/benefit analysis to determine how many nights a site will be surveyed. For our research using the number of bat passes as an activity index, the value of multiple nights of sampling is different. The number of passes expected per night is not altered by the number of nights sampled. Sampling multiple nights would yield a better estimate of the expected number of passes for that site by averaging over multiple nights (essentially reducing the standard error of the nightly estimate). The decision on how many nights a single site should be sampled comes down again to a cost/benefit analysis. If the cost to the sample size of replicate sites is zero when including multiple nights of sampling at each site, then multiple nights should be sampled. On the other hand, if there is a one to one cost in replication for every additional night sampled at a site, then it seems unlikely that multiple night sampling at one site would be wise. In our case we concluded that a single night per site was appropriate for this study. This allowed us to maximize the number of replicate sites per habitat type.

To determine habitat preferences, some index of the abundance of bats is needed. In studies employing acoustical bat detectors such as this, one index of bat activity is the number of call sequences recorded per night (Ford et al. 2005; McConville et al. 2013). The relationship between the number of call sequences per night and bat density is the subject of ongoing research (Adams et al. 2015). At this time there is no way to convert calls by night into bat density; however, we will assume that high numbers of bat passes per night are positively correlated with bat density. There is high variance in the number of calls per night even at one spot, or over a small area. This may relate to factors such as the location of maternity roosts or
flyways in the forest. To reduce the impact of outliers we log-transformed the data to form the variable Activity Index. Because of zeros in the number of call sequences per night, one was added to all call sequence counts before log-transformation.

**Predictor variables measured for each site**

**Habitat:** All microphones were placed in one of 4 habitat categories: Woods (microphone in the woods, n=39); Creek (microphone in the woods and within 5 meters of a permanent stream, n=12); Edge (microphone placed 5 meters in the open away from the edge of forest’s canopy, n = 21); Open (microphone placed in the open more than 20 meters from the edge of forest, n=8).

**Locality:** Sites were grouped into six named localities for analysis to determine possible geographic effects (groupings shown in Fig. 2).

The following landscape variables were measured using Google Earth Pro except for Area2000. Area2000 was measured using the 2005 Nebraska land use map (CALMIT, University of Nebraska-Lincoln and hereafter referred to as Calmit map) and ArcMap 10 (ESRI, Redlands, California).

**Area100:** Proportion of area within 100 m radius of site covered by forest as determined by outlining forested areas by hand within 100 m bounding circle in Google Earth Pro. This measure is the “ring statistic” used by Wiegand et al. (1999).

**Area500:** Proportion of area within 500 m radius of site covered by forest.

**Area2000:** Proportion of area within 2000 m radius of site covered by forest. We calculated Area2000 using the Calmit map. This map is based on 28.5 x 28.5 m raster data. For each site classified as Woods in our study we used ArcMap 10 to calculate Area2000 based on a circular pattern of radius of 71 rasters (approximate radius of 2000 m). We also calculated Area2000 for every raster point within Cass and Sarpy counties classified as forest using the Calmit map. To show the distribution of Area2000 we used the histogram function hist() from R with break points set every 0.1 from 0 to 1. This yielded 10 bins of Area2000 with centers at every 0.1 from 0.05 to 0.95.

**Outline100:** Using an image from Google Earth a 100 m circle was drawn with the recording site at the center. Then an outline polygon was traced by hand along the edges between the open and woodland habitats within the circle. The combined length of these outlines is Outline100.

**Outline500:** The same as Outline100 except based on a circle with radius 500m.

**DistWoods:** Distance to forest edge from site (if site is within forest, distance to edge is recorded as a negative). When testing hypothesis 4, only sites in Woods are included in the analysis to determine the possible impact of distance to open habitat from within woods.

**DistWater:** Distance to nearest water from site as determined by visual inspection on Google Earth.

**Statistical Analyses**

All statistical analyses were done in R statistical package (R Development Core Team 2008). The Activity Index variable was used as the dependent variable in an analysis of covariance using all variables in a log-transformation linear regression (modeled with the linear regression lm() program in R). There were two other viable regression alternatives: negative binomial regression and logistic regression. We considered the alternatives and ran full analyses with all three approaches. The use of the log-transformation seemed to deal with the problem of outliers more effectively than the negative binomial method. The logistic regression also dealt effectively with outliers; however, we felt useful quantitative information was discarded when the data were reduced from number of bat passes to simple presence/absence. Therefore, while there is general agreement among all methods of analysis, the approach we preferred was the log-transformation linear regression.

We used a stepwise procedure to eliminate variables from the full model (program step() within R) to find the best model. To determine the relative importance of variables in our multiple regression, we used calc.relaimpo (within the relaimpo R package). In our analysis we specified the lmg method, which uses a method of averaging sequential sums of squares over orderings of regressors to assess relative importance of variables.

Woods was used as the baseline state for the Habitat variable and Font (Fontenelle Forest) was used as the baseline for the Locality variable. In a sense this makes Woods and Font the control states that other habitats and localities are measured against. Therefore the coefficients for the other Habitat levels are given as additions or subtractions from the baseline of Woods.

**Results**

**Model creation**

When all Habitat types were included, all interaction terms and the variables Area100, Area2000, DistWoods, DistWater, Outline100 and Outline500 were eliminated...
Table 1. Best regression models (after stepwise elimination procedure) for Activity Index, based on acoustic detection of the Northern Long-eared Myotis (*Myotis septentrionalis*), in eastern Nebraska where part A includes all habitats types and part B includes only woods habitat type.

| Part A | Estimate | Std. Error | t value | Pr(>|t|) |
|--------|----------|------------|---------|----------|
| Intercept (Woods:Font) | 1.79 | 0.61 | 2.94 | 0.0045 ** |
| Area500 | 2.26 | 0.69 | 3.28 | 0.0016 ** |
| Habitat:Creek | 0.93 | 0.35 | 2.66 | 0.0096 ** |
| Habitat:Edge | -0.43 | 0.29 | -1.47 | 0.1469 |
| Habitat:Open | -1.25 | 0.43 | -2.91 | 0.0049 ** |
| Locality:Neale | -1.81 | 0.45 | -4.05 | 0.0001 *** |
| Locality:PRSP | -1.32 | 0.63 | -2.1 | 0.0393 * |
| Locality:Rakes | -1.76 | 0.55 | -3.21 | 0.0020 ** |
| Locality:Tem | -1.14 | 0.54 | -2.11 | 0.0382 * |
| Locality:WW | -0.85 | 0.5 | -1.7 | 0.0939 |

| Part B | Estimate | Std. Error | t value | Pr(>|t|) |
|--------|----------|------------|---------|----------|
| Intercept | 0.25 | 0.41 | 0.62 | 0.54 |
| Area2000 | 5.37 | 1.37 | 3.91 | 0.0004 * |

Based on the stepwise procedure. The variables remaining in this model were Area500, Habitat, and Locality (Table 1A). Based on the results from calc.relaimpo, we found that the relative importance of the variables were 21% Area500, 34% Habitat, and 45% Locality. The adjusted $r^2$ for this analysis was 0.49.

When the regression analysis is repeated with only sites classified as Woods, our results are different (Table 1B). All independent variables were eliminated by the stepwise procedure except Area2000. The adjusted $r^2$ for this analysis was 0.27. Activity Index is positively correlated with Area2000, but there is considerable variation (Fig. 3). Transforming the logarithmic Activity Index back to bat passes illustrates that the regression line is exponentially increasing as a function of Area2000 (Fig. 4A).

Figure 3. Activity index, based on acoustic detection of the Northern Long-eared Myotis (*Myotis septentrionalis*), increases as the proportion of forest within Area2000 increases.

Figure 4. Graph A shows the frequency of forest rasters for Area2000 in Cass and Sarpy Counties. The line is the regression’s prediction of activity of the Northern Long-eared Myotis (*Myotis septentrionalis*) transformed back to the number of bat passes per night. The regression line is shown in gray for Area2000 values above 0.5 because we have no data for such highly forested sites. Reflecting the highly fragmented nature of the forests in eastern Nebraska, we found no sites with Area2000 above 0.60. Graph B shows the total number of bat passes predicted in each bin class of forest coverage for Area2000.
The histogram in Figure 4A shows the frequency of forest rasters in Cass and Sarpy Counties by Area2000 bins. In this fragmented farmscape, small and medium sized woodlots are more common than large forests; no raster had an Area2000 over 0.6. Our regression indicates sites with high Area2000 would have far higher bat passes per night, and by inference, higher bat density, but these sites are rare in Cass and Sarpy Counties. If the number of rasters in each bin of the histogram is multiplied by the expected bat passes for that Area2000, a measure of the total bat passes for each bin is generated (Fig. 4B). The distribution of total bat calls by Area2000 indicates that for these counties, sites with intermediate values of Area2000 produce the most calls in aggregate. Small fragments of forest produce few expected calls because of low use by M. septentrionalis while larger forests produce fewer total calls because these larger forests are not common.

**Hypothesis 1**

*M. septentrionalis*, as a forest species, will avoid open fields and croplands. This hypothesis is supported (Table 1, coefficient = -1.25, *P* = 0.005) as activity of *M. septentrionalis* was significantly less in Open sites versus Woods sites of similar Locality and Area500. The average number of call sequences per night at Open sites is 0.12, while at Woods sites it is 11.8, an almost 100 fold increase. A visual representation of the avoidance of open habitat can be seen in figure 5. There is a near perfect step function of Activity Index at the transition from forest to open habitat.

**Hypothesis 2**

Activity of *M. septentrionalis* will be higher at woodland sites that are in areas with higher total coverage by forest. This hypothesis is supported (Table 1B, *P* = 0.0004). The regression between activity and area of forest is highly significant, but there is considerable variation around the regression line (*r^2* = 0.27). Note that the regression line is curvilinear in Figure 4A and linear in Figure 3 because in Figure 3 the number of bat passes has been log transformed to Activity Index.

**Hypothesis 3**

*M. septentrionalis* prefers forest edges. This hypothesis is not supported because activity of *M. septentrionalis* is not significantly higher at Edge sites (Estimate = -0.43; *P* = 0.15, Table 1). Further, the coefficient is negative and indicates less activity in edge habitats.

**Hypothesis 4**

*M. septentrionalis* avoids forest near edges. This hypothesis is not supported. For forested sites the distance out to the edge was not a significant predictor of Activity Index (*P* = 0.47). Note in figure 5 there is no apparent relationship between distance to edge of woods and Activity Index for negative values of distWoods (sites that are in the forest).

**Hypothesis 5**

*M. septentrionalis* prefers woodland streams over woodland sites without streams. The hypothesis is supported (Table 1, coefficient = 0.93, *P* = 0.01). The positive coefficient of 0.93 for Creek indicates a higher activity along creeks than Woods. As an example, the number of call sequences per night at Creek sites for Locality WW and Area500 of 0.5 is predicted to be about 2.8 times higher than activity found at Woods sites with the same Area500.

**Hypothesis 6**

There are important Locality differences in the activity of *M. septentrionalis*. Table 1A lists the results with some statistically significant differences among Localities. Therefore, when all habitat types are included, the hypothesis is supported. However if the analysis is restricted to Woods sites only, the statistical importance of Localities disappears (Table 1B).

**Discussion**

Our regression model contains variables Area500, Habitat and Locality when all habitat types are included, with Locality as the most important variable based on the relaimpo R package analysis. Area2000 emerges as the only significant independent variable when the analysis is restricted to only sites in Woods. The loss of Locality from the model is probably related to a problem of correlation of Locality and Area2000. Some Localities are more heavily forested than others and tend to have higher Area2000 values. This multicollinearity among independent variables such as Area2000, Area500, and Locality makes further interpretation of analyses difficult.

Our analysis indicates that wooded sites with higher Area2000 support exponentially more *M. septentrionalis*. This is a simple model consistent with the findings of Henderson et al. (2008). This result indicates that large forests are important to *M. septentrionalis*. However, the biological mechanism behind the correlation of forest coverage within Area2000 and bat activity is not clear. One possible explanation could have been based on hypothesis 4: core forest away from the forest–open ecotone is superior habitat for *M. septentrionalis*. However, this hypothesis was not supported by our analysis. Another possible explanation centers on the difference in small forest patches versus mid and large patches. In Nebraska’s
farmscape, sites with the lowest Area2000 are often hedgerows or narrow riparian habitats. Lower activity at such sites might reflect their role as occasional corridors for movement rather than foraging areas or sites for maternity colonies (Henderson and Broders 2008).

A critical question about larger forests remains unanswered; do large forest patches support more activity, and hence larger densities of *M. septentrionalis*, than intermediate-sized forests? If so these large blocks of forest could be key resources for the species. Unfortunately we cannot predict the expected activity in such large forests because they do not now exist in eastern Nebraska. Higher Area2000 values may produce further exponential increases in activity or there might be an asymptotic leveling off of activity. Such a leveling off would mean that the relationship between Area2000 and bat activity is a result of the dichotomy of tiny forests on one hand and midsized and larger ones on the other. The answer to this question is important because it has consequences for the management of *M. septentrionalis*. If bat density levels off with increasing forest size, then there would be little benefit to working towards the difficult task of creating larger forest preserves. A series of intermediate-sized forest patches, of similar total area, would serve the same purpose. On the other hand, if bat density continues to increase exponentially as patch size increases from intermediate to large forests, there might be management justification in attempting to create large forest preserves for this species.

This rarity of larger forest in our study area means that most *M. septentrionalis* individuals are living in smaller forests with Area2000 centered at 30% forest coverage (Fig. 4B). This pattern of activity does not address the role that different forests are playing in survival and reproduction of this species. It is possible that the majority of reproductive females are rearing young in higher Area2000 sites that serve as source habitats (Pulliam 1988), while low Area2000 sites are disproportionately inhabited by males and non-reproductive females. However this important issue cannot be addressed with our data and must await further research.

*Myotis septentrionalis* avoided open areas in our study, which is consistent with other studies (Patriquin and Barclay 2003). We also did not observe a spike in activity at the forest's edge for *M. septentrionalis*. This result is contrary to Jantzen and Fenton (2013) who found a peak of activity for *M. septentrionalis* at the forest-field edge. In our study, there is a clear step function in a narrow transition zone between open and forest habitat (Fig. 5). Once in the forest, there is no obvious increase or decrease in activity as a function of distance to forest edge. This is consistent with the view of *M. septentrionalis* as a strict, or nearly so, forest species.

![Figure 5. Activity index of the Northern Long-eared Myotis (*Myotis septentrionalis*) was highest at forested sites (green), lower at edge sites (blue), and lowest at open sites (red). In the forest the negative distances indicate distance from recording site in the forest to the nearest opening. All distances were subject to a slight jitter so overlapping circles would be revealed.](image)

Patriquin and Barclay (2003) noted that *Myotis lucifugus* preferred more open areas than *M. septentrionalis* and was more abundant than *M. septentrionalis* at their study area. In our study area there were few *M. lucifugus* (based on few recordings of this bat by our detectors). If there is any ecological release when *M. lucifugus* is less common, then *M. septentrionalis* might shift habitat use towards open areas. Our analysis indicates that *M. septentrionalis* is almost completely a forest species in our study area; it rarely ventures more than a few meters from the forest (Fig. 5). Therefore, if there is any habitat shift by *M. septentrionalis* to more open sites when its potential competitor, *M. lucifugus*, is uncommon, then it must be slight. Although activity is higher at sites adjacent to streams as predicted by Henderson and Broders (2008), stream effects might be limited to areas in the immediate vicinity of water. For example, the distance to water is not a significant predictor of Activity Index at Woods sites. Also, *M. septentrionalis* is found in woods well away from water sources, which aligns with results of Owen et al. (2003). Further research would be useful to determine the role of streams in habitat selection by *M. septentrionalis*. Many questions remain, but our study helps to clarify habitat use of *M. septentrionalis* in a shredded farmscape, and should be useful when considering monitoring and conservation strategies for this federally threatened species.
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