



Weather as a proximate explanation for fission–fusion dynamics in female northern long-eared bats



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Fission–fusion dynamics appear common among temperate bats where females form roost groups that change in size and composition, as females switch roosts almost daily. One hypothesis for frequent roost switching is that females move to find suitable thermal conditions as ambient conditions change. Tests of this hypothesis have, however, been conducted mostly at roosts in artificial structures where microclimate is relatively stable. The goal of our study was to determine whether roost switching and roost use by northern long-eared bats, *Myotis septentrionalis*, that roost in trees are related to ambient conditions. We used generalized linear fixed effects models to explore the influence of roost characteristics and changes in ambient conditions on the likelihood of roost switching. We used canonical correlation analyses to examine the relationship between ambient conditions and roost characteristics. Roost switching was indeed linked to ambient conditions together with characteristics of roosts on the previous day; the best descriptors of roost switching differed between the two geographical regions we analysed. In Nova Scotia, females were less likely to switch roosts when it rained, particularly if they were in roosts below surrounding canopy whereas they were more likely to switch roosts when they were in roosts of high decay. Females roosted in shorter trees in earlier decay classes on warm days, as well as on windy and rainy days. In Kentucky, females were more likely to switch roosts at high temperatures, particularly when they were in roosts in high decay. Females roosted in shorter, decayed trees on warm days, and in less decayed trees with small diameter on windy and rainy days. Our results suggest bats switch roosts in response to changes in ambient conditions to select suitable roosting conditions, which may explain some of the proximate factors shaping fission–fusion dynamics of bats.

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Fission–fusion social dynamics, where group size and composition change over time, have been observed in elephants, cetaceans and some primates (Aureli et al., 2008), as well as in several species of bats (Johnson, Ford, & Edwards, 2012; Johnson, Kropczynski, Lacki, Langlois, 2012; Kerth, 2008; Popa-Lisseanu, Bontadina, Mora, & Ibáñez, 2008). In temperate regions, where fission–fusion dynamics in bats appear common, females move to summer breeding areas following hibernation and gather to give birth and raise offspring (Kerth, 2008; Kerth, Perony, & Schweitzer, 2011; Kunz & Lumsden,

2003). Males roost separately from female maternity groups, either alone or in small all-male groups (reviewed in Patriquin & Ratcliffe, 2016). Throughout the summer, females regularly move among roosts, but also form long-lasting social relationships based, in part, on age and relatedness (Johnson, Kropczynski et al., 2012; Kerth, 2008; Kerth et al., 2011; Patriquin, Leonard, Broders, & Garraway, 2010, 2013; Popa-Lisseanu et al., 2008). Reasons for roost switching, which produces the variation in group size and composition typical of fission–fusion dynamics, are not, however, fully understood (reviewed in Patriquin & Ratcliffe, 2016).

Female bats are likely to switch roosts for multiple reasons. For example, females may move among roosts to reduce ectoparasite loads and predation risk (Bartonička & Gaisler, 2007; Bartonička & Růžicková, 2013; Lewis, 1996; Patterson, Dick, & Dittmar, 2007;

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Reckardt & Kerth, 2006; Threlfall, Law, & Banks, 2013), minimize distances between roosts and ephemeral prey (Lewis, 1995) and facilitate social connections and information sharing among a network of conspecifics (Kerth & van Schaik, 2011; Willis & Brigham, 2004). Because conditions inside roosts can vary over time, females may also move to find roosts that minimize thermoregulatory costs and maximize offspring development under particular ambient conditions (Barclay & Kurta, 2007).

Although moving to find suitable thermal conditions is likely to be important, direct evidence that bats switch roosts, particularly in natural conditions, in response to changes in ambient conditions is limited. For example, roost characteristics often correlate with ambient conditions (Barclay & Kurta, 2007; Clement & Castleberry, 2013; Pretzlaff, Kerth, & Dausmann, 2010), leading to the assumption that females switch roosts in response to changing ambient conditions that result in a mismatch between roost conditions and weather conditions. Indeed, females have been observed switching roosts, or among locations within roosts, in response to changing ambient temperatures, but only when temperatures exceed 30 °C (e.g. Ellison, O'Shea, Neubaum, & Bowen, 2007; Lourenço & Palmeirim, 2004). In these cases, however, bats were living in artificial structures, where roost temperature was typically warmer than ambient temperature, less variable than in natural roosts and provided greater protection from precipitation (Campbell, Coulson, & Lumsden, 2010; Clement & Castleberry, 2013; Lausen & Barclay, 2006; Lourenço & Palmeirim, 2004) and, therefore, roost switching was less frequent (Trousdale, Beckett, & Hammond, 2008). A stronger relationship between changes in ambient conditions and roost switching may then be expected for species using natural roosts, where conditions are more variable. The only study to directly examine this relationship in natural roosts found that ambient conditions did not influence roost switching (Lewis, 1996). However, this study did not consider the characteristics of the roosts being used when ambient conditions changed, factors that are likely to affect the thermal conditions experienced by bats and therefore the probability of switching. In other words, while some bats do appear to switch roosts when weather conditions change, they do not necessarily switch in response to all changes, suggesting that the quality of the roost at the time of the change, together with the magnitude of change, may affect these decisions.

At the same time, ambient conditions and the types of roosts available vary across the geographical range of a species, which may lead to intraspecific variation in roost use and roost-switching behaviour. For example, juvenile Daubenton's bats, *Myotis daubentonii*, occupying buildings with warmer temperatures switch roosts less frequently than those occupying tree roosts with comparatively cooler temperatures (Ngamprasertwong, Piernney, Mackie, & Racey, 2014). Female western long-eared bats, *Myotis evotis*, in Alberta, Canada, are exposed to different temperatures in the prairies than in the mountains; correspondingly they use roosts with different thermal properties and they use torpor to different degrees (Chruszcz & Barclay, 2002; Solick & Barclay, 2007). At larger spatial scales, variation in roost use by long-legged bats, *Myotis volans*, across the Pacific Northwest of the United States has been attributed to regional differences in climate (Lacki, Bakker, & Johnson, 2010). Similarly, a meta-analysis of existing studies suggests that roost use of Indiana bats, *Myotis sodalis*, and northern long-eared bats, *Myotis septentrionalis*, also varies across the United States (Lacki & Cox, 2009). More recently, Fabianek, Simard, and Desrochers (2015) performed a meta-analysis of 34 studies examining roost use of various tree-cavity roosting species across North America and included mean temperature. Their analyses revealed that, regardless of location, bats select roosts based on tree diameter, tree height, canopy cover, snag density and elevation, but

these characteristics differed between northern and southern populations due to differences in mean temperature (Fabianek, Simard, & Desrochers, 2015). Thus, at various spatial scales, bats show intraspecific variation in roost use.

At least one study has examined geographical variation in roost use and roost switching with respect to ambient conditions. In Europe, female greater mouse-eared bats, *Myotis myotis*, tend to use caves and mines with cooler and more stable microclimate in more southern populations (Portugal) and attics with warmer and more variable microclimates at more northern latitudes (Germany), which the authors attribute to differences in regional climate (Rodrigues, Zahn, Rainho, & Palmeirim, 2003). Correspondingly, females in the southern location rarely move among locations within caves and mines whereas they move regularly among locations within attics (Rodrigues et al., 2003). These observations, however, are complicated by comparisons of two different roost types that vary in relative permanence and availability, which in turn affect roost fidelity (e.g. Johnson, Ford et al., 2012). Thus, a study examining intraspecific geographical variation in daily roost use and roost switching in response to daily changes in ambient conditions controlling for roost type (e.g. trees, rocks or buildings) is warranted.

Determining whether species behave similarly across their range has both theoretical and practical implications. For instance, if bats in different parts of their range respond differently to changes in ambient conditions, this could offer insight to the proximate explanations for differences in social structure, which is driven in large part by roost switching. In addition, as Foster, Wund, and Baker (2015, page 406) argue, a better understanding of geographical variation in behaviour may allow us to 'accurately anticipate effects of anthropogenic environmental modification on the persistence and evolution of animals'.

The goal of our study was to test the hypothesis that ambient conditions influence, at least in part, roost-switching behaviour of female northern long-eared bats in natural roosts (trees). Similar to other temperate bat species, female northern long-eared bats return to summer breeding areas following hibernation, where they raise young in tree cavities (Caceres & Barclay, 2000). During this time, females live in groups with fission–fusion dynamics where they form associations within groups that vary in size and composition, as females move regularly between day-roosts (Garroway & Broders, 2007; Patriquin et al., 2013, 2010; Silvis, Kniowski, Gehrt, & Ford, 2014). Previous work found that females in different reproductive condition have different roost preferences, with lactating females preferring roosts in tall trees with a greater distance between the roost exit and the surrounding canopy height and low surrounding tree density compared to females in pre- and postlactating conditions (Garroway & Broders, 2008). It is not known, however, how changing ambient conditions affect the likelihood of roost switching across different reproductive periods. Understanding geographical variation in roost use of northern long-eared bats is particularly important as they are now federally listed as endangered in Canada (Committee on the Status of Endangered Wildlife in Canada, 2013) and threatened in the United States (United States Fish and Wildlife Service, 2016) due to their rapid population declines as a result of the spread of a lethal fungal pathogen, *Pseudogymnoascus destructans* (formerly *Geomyces destructans*) during hibernation. We therefore tested the following predictions: (1) changes in ambient weather conditions affect the likelihood of roost switching; (2) the relationships between roost use, roost switching and ambient conditions vary between populations in different parts of the species' distribution; (3) characteristics of roosts selected by females are correlated with ambient conditions.

METHODS

General Site Descriptions

Nova Scotia

We conducted our study from early June to mid-August, 2005–2007 in Dollar Lake Provincial Park (DLPP), Nova Scotia, Canada (44°55'N, 63°19'W). The park borders a large (27 km²) lake and is characterized as mixed-wood old growth Acadian forest, which consists of uneven-aged stands. Stands are made up primarily of red maple, *Acer rubrum*, eastern hemlock, *Tsuga canadensis*, eastern white pine, *Pinus strobus*, and yellow birch, *Betula alleghaniensis*, as well as some older sugar maple, *Acer saccharum*, and younger or regenerating maple, birch, black spruce, *Picea mariana*, and red spruce, *Picea rubens*, and dead or dying trees (Loo & Ives, 2003). Research at DLPP was conducted according to the standards of the Dalhousie University Committee on Laboratory Animals (2004-160) and the Nova Scotia Department of Natural Resources Wildlife Act.

Kentucky

We conducted our study from late May to July, 2011 and 2012, on the Fort Knox Military Reservation (FKMR) in Meade, Bullitt, and Hardin counties, Kentucky, U.S.A. (37°53'N, 85°54'W). FKMR is characterized as a western mixed-mesophytic association (Braun, 1950), with second- and third-growth forests dominated by white oak, *Quercus alba*, black oak, *Quercus velutina*, chinkapin oak, *Quercus muehlenbergii*, shagbark hickory, *Carya ovata*, yellow poplar, *Liriodendron tulipifera*, white ash, *Fraxinus americana*, and American beech, *Fagus grandifolia*, in the overstory, and sassafras, *Sassafras albidum*, redbud, *Cercis canadensis*, and sugar maple in the understory (Cranfill, 1991). Research at FKMR was approved by the Virginia Polytechnic Institute and State University Institutional Animal Care and Use Committee (protocol number 11-040-FIW) and carried out in accordance with state requirements for capture and handling of wildlife (Kentucky Department of Fish and Wildlife Resources permit numbers SC1111108 and SC1311170).

General Methods

We captured bats between dusk and sunrise using mist nets (Avinet, Dryden, NY, U.S.A.) and harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia). We followed all capture and handling protocol guidelines according to the American Society of Mammalogists (Sikes, Gannon, & The Animal Care and Use Committee of the American Society of Mammalogists, 2011). We identified young of the year based on incomplete calcification of the epiphyseal gap on the fourth metacarpal (Anthony, 1988) and excluded them from analyses. We identified females as pregnant, nursing, or weaning by palpation of the abdomen, expression of milk from the nipples, or worn fur around the nipples with no expression of milk, respectively (Racey, 2009).

To locate roost trees, we attached radiotransmitters (LB-2, 0.31 g, and LB-2NT, 0.39 g: Holohil Systems Ltd, Woodlawn, ON, Canada) between the scapulae of female bats using surgical cement (Perma-Type Company Inc., Plainville, CT, U.S.A., or SkinBond, Smith and Nephew United Inc., Largo, FL, U.S.A.). We located roost trees and recorded movements by radiotracking females daily until transmitters fell off or the battery died (DLPP: mean = 6.7 days; range 1–24 days; FKMR: mean = 5.7 days; range 2–12 days). Comparison of movements of bats marked with passive integrated transponders (PIT-tags, also known as radiofrequency identification (RFID) tags) weighing 0.09 g relative to movements of bats with radiotransmitters suggests that radiotags had no detectable impact on female movement (Patriquin et al., 2010).

Because previous studies have demonstrated differences in roost-switching behaviour and roost use among females in different reproductive condition, we included reproductive condition as a variable in our analyses to control for possible differences. For instance, pregnant females are more likely than lactating females to select cooler or smaller-diameter roosts that facilitate torpor, presumably because delayed fetal development associated with torpor is less costly than reduced milk production (e.g. Barclay & Kurta, 2007; Dietz & Hörig, 2011; Dzal & Brigham, 2013; Klug & Barclay, 2013; Pretzlaff et al., 2010; Speakman, 2008). Lactating females may also be less likely to switch roosts because of the costs of transporting nonvolant young (Cryan, Bogan, & Yanega, 2001; Russo, Cistrone, & Jones, 2005). To assess potential differences in roost use and roost switching across the reproductive season in DLPP, we divided observations into three reproductive periods, gestation, lactation and weaning, based on the first capture of individuals in that reproductive stage. This approach was used because, in addition to tracking movements of radiotagged animals, individuals injected with PIT-tags were also observed whose reproductive status was not always known (see Patriquin, 2012, for details). This was a reasonable approach because capture data suggested that breeding was relatively synchronous during our study at DLPP, as females typically gave birth within 4 days of each other (K. Patriquin, personal observation). In FKMR, however, reproductive status reflected the status of each individual as data were collected from radiotagged animals of known reproductive status.

To characterize ambient conditions, we obtained 12 measures of daily ambient conditions from an Environment Canada weather station at the Halifax Stanfield International Airport (44°52'N, 063°30'W; ≈ 20 km from DLPP) and Godman Army Airfield weather station (located on FKMR). They included: (1) daily maximum temperature (°C), (2) daily mean temperature (°C), (3) daily minimum temperature (°C), (4) total daily rainfall (mm), (5) temperature at sunset (°C), (6) presence of precipitation at sunset, (7) wind speed at sunset (km/h), (8) barometric pressure at sunset (kPa), and (9–12) the same measures as (5)–(8) but at sunrise.

To minimize disturbance to bats, we measured roost tree and site characteristics (herein referred to simply as roost characteristics) either when bats left a given tree or at the end of the season. To characterize roosts used by females, we measured nine roost and site characteristics thought to affect the thermal properties of roosts through exposure to or protection from sun, wind or rain (Barclay & Kurta, 2007), including (1) roost tree height (m), (2) roost height (m), (3) tree species, (4) diameter at breast height (dbh) (cm), (5) percentage of bark remaining on the tree, (6) decay stage, (7) average dominant canopy height (m), (8) canopy height relative to roost height (m) and (9) average canopy cover (%) (for more detailed descriptions of DLPP and FKMR roost measurements, respectively, see Patriquin, 2012; Silvis, Ford, Britzke, Beane, & Johnson, 2012). Roost cavities were mostly inaccessible, so we could not measure internal temperature or humidity. We did not compare characteristics of roost trees to random trees as we were interested in the relationship between roost characteristics and ambient conditions, and not female preference for particular roost characteristics.

Statistical Analyses

To describe overall patterns of roost switching, for bats observed on at least two consecutive days, we estimated frequency of roost switching ((number of switches/total number of days tracked) × 100) and residency time (number of consecutive days a female remained in a particular roost). We also examined whether females in different reproductive periods differ in frequency of roost

switching by comparing the percentage of observations where females switched roosts during gestation, nursing and weaning.

To reduce the number of variables for consideration in assessment of roost switching, we performed some preliminary exploratory modelling using data from DLPP wherein we assessed multicollinearity of weather variables and roost characteristics using principal components analysis (see Patriquin, 2012, for details). Based on this exploratory modelling, together with evidence from previous studies (e.g. Callahan, Drobney, Clawson, 1997; Lourenço & Palmeirim, 2004), we selected the following weather variables for the DLPP and FKMR data sets: (1) maximum daily temperature ($^{\circ}\text{C}$), (2) total daily rainfall (mm), (3) temperature at sunset ($^{\circ}\text{C}$), (4) wind speed at sunset (km/h) and (5) barometric pressure at sunset (kPa). We used the following roost and site characteristics in subsequent analyses: (1) roost tree height (m), (2) decay stage, (3) diameter at breast height (dbh) (cm), (4) average canopy cover (%) and (5) canopy height relative to roost height (m).

We modelled roost-switching behaviour using generalized linear mixed effects models with a binomial link function. Based on the premise outlined above, we created a set of 50 a priori models (see [Supplementary Material](#)) that contained additive combinations of either weather variables, roost variables, or both. Because overall habitat and weather were different between our two locations and therefore may have differential effects on roost-switching behaviour, we analysed each data set separately but used the same set of models for each site. Our models represented hypotheses based on thermal limitations (minimum and maximum), overall thermal dynamics (mean), absolute weather conditions, nightly change in weather conditions (i.e. $\Delta y = y_t - y_{t-1}$; temperature, wind, barometric pressure), and their relationship to roost conditions on the previous day. Because we had repeated measurements on individual bats and repeated observations from within years, we included bat identity and year as random effects (intercept only). We controlled for reproductive condition by including it as a fixed effect in every model. We included reproductive condition as a fixed rather than random effect because we were directly interested in the effect of reproductive condition and because previous research indicated that this factor is related to roost selection and roost switching (Barclay & Kurta, 2007). After initial modelling efforts, we created post hoc models based on the best-supported models that included polynomial terms and plausible and biologically meaningful multiplicative interactions among variables. This allowed us to retain a relatively simple overall model list while still exploring more complex interactions among variables. To aid in model fitting and interpretation, we standardized all continuous input variables by subtracting the mean and dividing by a single standard deviation (Schielzeth, 2010). Although we measured decay class as an ordinal variable, initial modelling efforts showed that inclusion of decay class as an ordinal variable caused most models with more than three predictors to fail to converge. Because we believed decay class was an important descriptor of roost condition, we elected to use decay class as a continuous input variable, subjected to the same standardization as other continuous input variables. A set of simplified test models indicated a consistent relationship between decay class and roost switching whether or not decay was used as an ordinal or continuous predictor. We ranked models using Akaike's Information Criterion corrected for small sample size (AIC_c), the difference between the model with the lowest AIC_c and the AIC_c of the i th model (Δ_i) and Akaike's weights (w_i) (Burnham & Anderson, 2002). To account for uncertainty in the model selection process, we model averaged the best-supported ($\Delta_i < 4$) models for each data set using the natural averaging method (Grueber, Nakagawa, Laws, & Jamieson, 2011; Symonds & Moussalli, 2011). To better understand model fit, we also

calculated conditional and marginal pseudo- R^2 values following the method of Nakagawa and Schielzeth (2013).

To describe the relationship between the ambient conditions and roost characteristics listed above, we performed a canonical correlation analysis (CCA). In this analysis, we assessed covariance among a series of orthogonal combinations (dimensions) of ambient conditions and roost characteristics (Quinn & Keough, 2002): significant dimensions ($P < 0.05$) that explained at least 25% of the variance (covariance ≥ 0.25) represent the combination of ambient conditions and roost characteristics that best explained the types of roosts used under given ambient conditions (Hair, Black, Babin, & Anderson, 2010). We identified variables with large positive (≥ 0.3) or negative (≤ -0.3) standardized coefficients as variables that best explained the relationship between ambient conditions and roost characteristics within the significant dimensions. We examined the standardized coefficients to allow for a more direct comparison of the relationships among variables measured on different scales. We included year and day to determine whether the relationship between ambient conditions and roost characteristics varied with these factors.

We conducted all analyses using the R statistical program (R Development Core Team, 2014). We fitted generalized linear mixed effects models with package 'lme4' (Bates, Bolker, & Walker, 2014), performed model selection and averaging using package 'MuMIn' and conducted CCA using package 'candisc'.

RESULTS

General Patterns

Average maximum daily temperature and rainfall differed between DLPP and FKMR during our study periods, as did average temperature, minimum temperature, wind speed and barometric pressure at sunset (Fig. 1). Generally, it was warmer, drier and less windy in Kentucky compared to Nova Scotia. There were, however, short periods of intense rain in Kentucky (Fig. 1).

Nova Scotia

From 2005 to 2007, 59 adult female northern long-eared bats were radiotracked to 131 day-roost trees that were used for 370 bat-roost days. A bat-roost day represents the observed presence of a bat in a roost on a particular day. Specifically, we radiotracked 19 females to 42 roost trees in 2005, 19 females to 53 roost trees in 2006 and 21 females to 46 roost trees in 2007. Females were tracked for a mean of 5.2 consecutive days (range 2–16), with 76% of females tracked for at least three consecutive days. Females switched roosts from one day to the next a mean \pm SD of $58.2 \pm 35.1\%$ of occasions and had an average residency time of 1.50 ± 1.04 days. Females revisited at least 12% of the roosts used within summers and reused at least 25% of roosts between summers. The frequency with which females switched roosts varied with reproductive period; weaning females moved the most (mean \pm SD percentage of days females switched roosts = $78.0 \pm 34.6\%$; $N = 6$), followed by pregnant ($60.4 \pm 38.0\%$; $N = 29$) and nursing females ($53.8 \pm 34.3\%$; $N = 36$; note: some individuals were tracked across multiple reproductive periods, and therefore totals differ from the overall total number of unique individuals tracked). For a more detailed description of types of roosts used by females, see Patriquin (2012).

Kentucky

In 2011 and 2012, 108 adult female northern long-eared bats were radiotracked to 168 day-roost trees that were used for 601 bat-roost days. Specifically, we radiotracked 50 females to 104 roost trees in 2011, 58 females to 104 day-roost trees in 2012, seven of

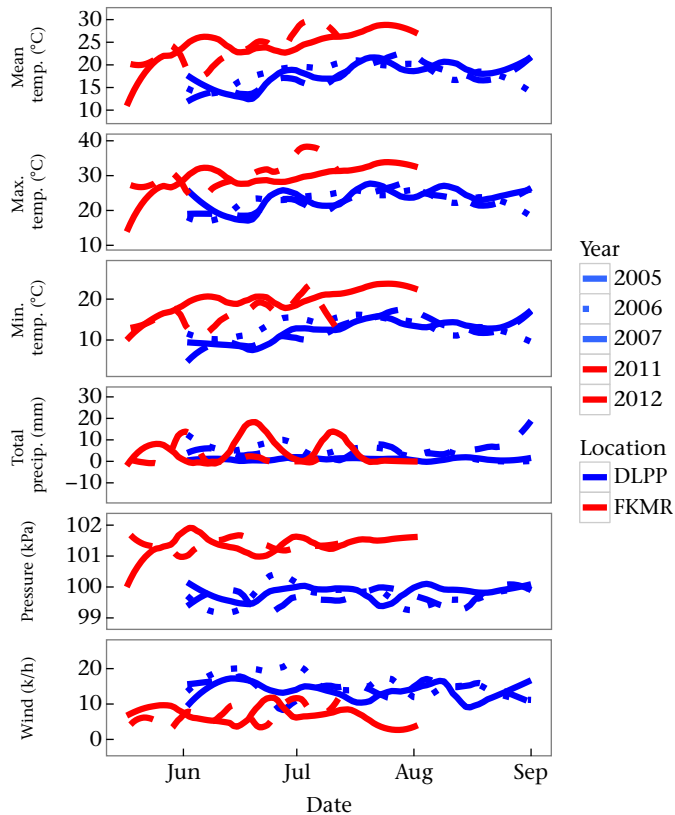


Figure 1. Ambient conditions used to model roost use and roost switching by female northern long-eared bats, *Myotis septentrionalis*, at Dollar Lake Provincial Park, NS, Canada, from 2005 to 2007, and at Fort Knox Military Reservation, KY, U.S.A., from 2011 to 2012.

which were previously used in 2011. Females were tracked for a mean of five consecutive days (range 2–13), with 83% of females tracked for at least three consecutive days. Females switched roosts from one day to the next a mean \pm SD of $63.1 \pm 34.5\%$ of occasions and had an average residency time of 1.67 ± 1.43 days. Females revisited at least 10% of the roosts used within summers and reused at least 23% of roosts between summers. The frequency with which females switched roosts varied with reproductive period; nonreproductive females moved the most (mean \pm SD percentage of days females switched roosts = $88.1 \pm 21\%$; $N = 6$), followed by weaning ($69.4 \pm 23.4\%$; $N = 10$) and nursing ($64.0 \pm 34.2\%$; $N = 73$) females,

Table 1

Best-supported ($\Delta_i < 4$) generalized linear mixed effects models describing roost switching by female northern long-eared bats in Dollar Lake Provincial Park, NS, Canada, from 2005 to 2007

Model ^a	df	logLik	AIC _c	Δ_i	w_i	R ² marginal	R ² conditional
Reproductive period+mean temperature+total precipitation+mean canopy cover+roost relative to canopy	8	-105.32	227.49	0.00	0.29	0.27	0.35
Reproductive period+total precipitation	5	-109.35	229.05	1.56	0.13	0.20	0.32
Reproductive period+total precipitation+change in wind speed+mean temperature+mean canopy cover+roost relative to canopy	9	-105.23	229.52	2.03	0.10	0.27	0.36
Reproductive period+minimum temperature+total precipitation+mean canopy cover	7	-107.65	229.96	2.46	0.08	0.23	0.34
Reproductive period+mean temperature+total precipitation+decay class	7	-107.96	230.57	3.08	0.06	0.22	0.35
Reproductive period+minimum temperature+total precipitation+decay class	7	-107.99	230.62	3.13	0.06	0.22	0.36
Reproductive period+mean temperature+total precipitation	6	-109.14	230.77	3.28	0.06	0.20	0.31
Reproductive period+minimum temperature+total precipitation	6	-109.22	230.93	3.44	0.05	0.20	0.31
Null	3	-122.18	250.50	23.01	0.00	0.00	0.17

Model parameters are given as well as the effective degrees of freedom (df), log likelihoods (logLik), Akaike's Information Criterion corrected for small sample size (AIC_c), difference in AIC_c value between top model and ith model (Δ_i), model support (w_i), and conditional and marginal pseudo-R². The null model has been included for reference.

^a All variables represent z-transformed data measured on the day prior to switching. For an explanation of each predictor and a list of all models, please refer to [Supplementary Material](#).

with pregnant females moving the least ($44.6 \pm 39.4\%$; $N = 17$; note: some individuals were tracked across multiple reproductive periods, and therefore totals differ from the overall total number of unique individuals tracked). For a more detailed description of types of roosts used by females, see [Silvis et al. \(2012\)](#).

Ambient Conditions and Roost Switching

Nova Scotia

There was considerable uncertainty in selecting a model that best explained variation in roost switching for northern long-eared bats at DLPP, as eight models had $\Delta_i < 4$ (Table 1). No post hoc models received substantial support (i.e. $\Delta_i > 4$); all competing models had marginal pseudo-R² values > 0.2 , with the best model having a value of 0.27. The averaged model included reproductive condition, mean temperature on the previous day, total precipitation on the previous day, average canopy cover on the previous day, an indicator for whether the roost was above or below canopy height, nightly change in wind, minimum temperature the previous day and the decay class of the roost (Table 2). In the averaged model, total precipitation the previous day had a larger effect size than decay class, with probability of roost switching decreasing with precipitation and increasing with decay stage. Among binary predictors, roost location relative to surrounding canopy had the largest effect size and indicated a decreased likelihood of switching when the roost was under canopy height.

Kentucky

No model describing roost switching for northern long-eared bats on FKMR received unequivocal support (Table 3). However, only two models were well supported; both were from the post hoc set and supported the presence of a multiplicative interaction between roost decay class and maximum temperature on the previous day. Marginal pseudo-R² values were > 0.20 for both competing models. The averaged model included reproductive condition, maximum temperature on the previous day, roost decay class, nightly change in temperature and an interaction between decay class and maximum temperature (Table 4). In the averaged model, maximum temperature and decay class had similar relative effect sizes and both indicated a positive relationship with roost-switching likelihood. Similarly, the interaction between maximum temperature and decay class indicated an increased likelihood of switching with increasing values of both conditions.

Table 2
Model-averaged parameter estimates of the best-supported ($\Delta_i < 4$) generalized linear mixed effects models describing roost switching by female northern long-eared bats in Dollar Lake Provincial Park, NS, Canada, from 2005 to 2007

	Estimate	SE	Adjusted SE	z	95% CI
(Intercept)	-0.503	0.328	0.331	1.522	(-1.151, 0.145)
Reproductive period: Pregnant	1.493	0.489	0.493	3.032	(0.528, 2.459)
Mean temperature	0.190	0.216	0.218	0.871	(-0.237, 0.616)
Total precipitation	-0.983	0.243	0.245	4.020	(-1.462, -0.504)
Mean canopy cover	-0.414	0.243	0.244	1.693	(-0.893, 0.065)
Roost relative to canopy	-1.098	0.516	0.520	2.112	(-2.117, -0.079)
Change in wind speed	0.080	0.187	0.189	0.424	(-0.29, 0.45)
Minimum temperature	0.066	0.222	0.223	0.296	(-0.372, 0.504)
Decay class	0.373	0.172	0.174	2.151	(0.033, 0.714)

Parameters with 95% confidence intervals that did not overlap zero are highlighted in bold. All variables represent z-transformed data measured on the day prior to switching.

Table 3
Best-supported ($\Delta_i < 4$) generalized linear mixed effects models describing roost switching by female northern long-eared bats at Fort Knox Military Reservation, KY, U.S.A., from 2011 to 2012

Model	df	logLik	AIC _c	Δ_i	w_i	R ² marginal	R ² conditional
Reproductive period+maximum temperature+decay class+change in temperature	10	-248.07	516.65	0.00	0.52	0.24	0.38
Reproductive period+maximum temperature+decay class	9	-249.45	517.33	0.67	0.37	0.22	0.38
Null	3	-274.85	555.75	39.10	0.00	0.00	0.29

Model parameters are given as well as the effective degrees of freedom (df), log likelihoods (logLik), Akaike's Information Criterion corrected for small sample size (AIC_c), difference in AIC_c value between top model and ith model (Δ_i), model support (w_i), and conditional and marginal pseudo-R². The null model has been included for reference. All variables represent z-transformed data measured on the day prior to switching.

Table 4
Model-averaged parameter estimates of the best-supported ($\Delta_i < 4$) generalized linear mixed effects models describing roost switching by female northern long-eared bats at Fort Knox Military Reservation, KY, U.S.A., from 2011 to 2012

	Estimate	SE	Adjusted SE	z	95% CI
(Intercept)	0.545	0.314	0.315	1.733	(-0.071–1.162)
Nonreproductive	1.748	0.932	0.935	1.870	(-0.084–3.58)
Weaning	0.135	0.516	0.518	0.261	(-0.88–1.149)
Pregnant	-0.557	0.402	0.403	1.380	(-1.347–0.234)
Maximum temperature	0.522	0.147	0.148	3.532	(0.232–0.812)
Decay class	0.552	0.145	0.146	3.788	(0.266–0.837)
Change in temperature	0.218	0.131	0.132	1.657	(-0.04–0.476)
Decay class + maximum temperature	0.463	0.164	0.165	2.811	(0.14–0.785)

Parameters with 95% confidence intervals that did not overlap zero are highlighted in bold. All variables represent z-transformed data measured on the day prior to switching.

Ambient Conditions and Roost Characteristics

Nova Scotia

In DLPP, tests of dimensionality indicated that two of the four canonical dimensions were statistically significant (Table 5). The first dimension had a canonical correlation of 0.40 between roost characteristics and ambient conditions while the second dimension had a correlation of 0.31 (Table 6), suggesting that

ambient conditions and roost characteristics were correlated. The canonical coefficients for the first canonical dimension were most strongly influenced by maximum temperature, temperature at sunset and tree height. Specifically, tree height was negatively correlated with maximum temperature and temperature at sunset. Also, the relationship between ambient conditions and roost characteristics varied with year and day (Table 6, Fig. 2a).

Table 5
Canonical dimensions used to explain the relationship between ambient conditions and the characteristics of roosts used by female northern long-eared bats, *Myotis septentrionalis*, at Dollar Lake Provincial Park, NS, Canada, from 2005 to 2007, and at Fort Knox Military Reservation, KY, U.S.A., from 2011 to 2012

Dimension	% Variance	Canonical correlation	Multivariate F	df1	df2	P
Dollar Lake Provincial Park						
1	50.83	0.40	2.56	24	569.85	0.000
2	27.79	0.31	2.03	15	453.13	0.012
3	19.79	0.27	1.66	8	330	0.107
4	1.59	0.08	0.34	3	166	0.799
Fort Knox Military Reservation						
1	89.84	0.55	4.92	24	953.59	0.000
2	7.42	0.19	0.89	15	756.79	0.577
3	1.75	0.09	0.45	8	550.00	0.889
4	0.99	0.07	0.44	3	276.00	0.725

Statistically significant outcomes are shown in bold.

Table 6

Canonical standardized coefficients for significant dimensions used to explain the relationship between ambient conditions and the characteristics of roosts used by female northern long-eared bats at Dollar Lake Provincial Park, NS, Canada, from 2005 to 2007, and at Fort Knox Military Reservation, KY, U.S.A., from 2011 to 2012

Variables	Dollar Lake Provincial Park		Fort Knox Military Reservation
	Coefficient 1	Coefficient 2	Coefficient
Climate			
Maximum temperature (°C)	0.55	–0.19	0.24
Total precipitation (mm)	–0.20	–0.83	0.01
Temperature at sunset (°C)	0.44	–0.12	0.81
Wind speed at sunset (km/h)	0.10	0.62	0.35
Seasonal and roost			
Year	–0.54	–0.62	–0.34
Day	0.53	–0.85	0.73
Tree height (m)	–0.62	–0.80	–0.05
Decay class	–0.17	–0.37	0.15
dbh (cm)	0.18	0.05	0.04
Mean canopy cover (%)	0.03	–0.16	–0.05

Canonical variables with coefficients ≥ 0.3 (shown in bold) had the greatest influence on each dimension.

The canonical coefficients for the second canonical dimensions were most strongly influenced by total precipitation, wind speed, tree height and decay class. Specifically, tree height and decay class were positively correlated with total precipitation and negatively correlated with wind speed (Table 6). Again, the relationship between ambient conditions and roost characteristics differed with year and day (Table 6).

Kentucky

In FKMR, tests of dimensionality indicated that only one of the four canonical dimensions was statistically significant (Table 5). This dimension had a canonical correlation of 0.59 between roost characteristics and ambient conditions (Table 6). The canonical coefficients indicated that this canonical dimension was most strongly influenced by temperature at sunset and wind speed, whereas none of the roost characteristics had a strong influence. Instead, most of the relationship was explained by variation with year and day (Table 6, Fig. 2b).

DISCUSSION

Our results support our hypothesis that roost switching by female northern long-eared bats is at least partially influenced by ambient conditions and suggests that the relative importance of particular conditions varies geographically. In the cooler climate of Nova Scotia, females were less likely to switch roosts when precipitation increased from one day to the next, when they were in roosts below the canopy, but they were more likely to switch if they were in roosts of high decay. By contrast, in the warmer climate of Kentucky, females were more likely to switch roosts when temperature increased from one day to the next when they were in roosts with high decay. These findings support the hypothesis that there is selection pressure for temperate bats to select roosts with microclimates buffered against suboptimal conditions.

Similar to other bats that show reduced activity in rain (Baerwald & Barclay, 2011; Vonhof & Barclay, 1996), female northern long-eared bats in Nova Scotia were less likely to move with increasing rain. Although we did not track bats at night to confirm whether they emerged to forage or move, the costs of moving in the rain may increase thermoregulatory costs (Voigt, Schneeberger, Voigt-Heucke, & Lewanzik, 2011), or interfere with echolocation and navigation (Griffin, 1971), which may outweigh the benefits of moving to roosts that may otherwise provide more optimal thermal conditions. Moreover, it is generally argued that aerial-hawking bats, like big brown bats, *Eptesicus fuscus*, are less likely to emerge during inclement conditions due to lower insect availability (e.g. Ciechanowski, Zajac, Vilas, & Dunajski, 2007).

Alternatively, females may locate suitable roosts before the onset of inclement weather, thus precluding the need to move in rain. Indeed, female northern long-eared bats in Nova Scotia typically roosted in tall trees with cavities below the canopy on wetter, cooler, windier days. Thermal conditions are generally more stable in these types of roosts and females would be protected from inclement weather (reviewed in Barclay & Kurta, 2007; Pretzlaff et al., 2010). However, when females were in roosts of high decay, they were in fact more likely to switch roosts despite precipitation, again suggesting they were avoiding exposure to inclement weather as roosts in higher decay often have more crevices and cracks and thus more exposure to rain (Silvis, Ford, & Britzke, 2015). Avoiding inclement weather was likely less of a concern for females in Kentucky where it was warmer and rainfall events, while at times intense, were often of shorter duration than in Nova Scotia.

Ambient temperature has a strong influence on thermoregulation in bats (Speakman & Thomas, 2003), thus it is not surprising that females switched roosts when temperatures changed. Yet, only female northern long-eared bats in the southern location moved when temperatures changed. There, females moved when temperatures increased, particularly when bats were in roosts with high decay where temperatures were probably higher on hot days compared to roosts in live trees, which are generally better insulated against changes in ambient conditions (Coombes, Bowman, & Garroway, 2010). Temperatures may have exceeded the upper thermoneutral zone for northern long-eared bats in Kentucky, as documented for other bat species that switch only when temperatures exceed 30 °C (Ellison et al., 2007; Lourenço & Palmeirim, 2004; Vonhof & Barclay, 1996), but likely did not exceed their upper thermoneutral zone in Nova Scotia. Indeed, average maximum daily temperature reached 30 °C in Kentucky but only 23 °C in Nova Scotia.

Roost switching by female northern long-eared bats was therefore related, at least in part, to ambient conditions, presumably to select roosts with optimal thermal conditions. Although we were unable to measure thermal conditions in the roosts used by our populations, previous work has demonstrated that females select characteristics that minimize thermoregulatory costs and negative fitness consequences of selecting suboptimal roosts (Lausen & Barclay, 2006). However, the uncertainty in selecting the best-fit models described above as well as the relatively low conditional pseudo- R^2 values suggest additional factors not measured in our study likely also influence roost switching by female northern long-eared bats.

Although females generally moved in response to changes in ambient conditions and the characteristics of roosts were correlated with ambient conditions, our models suggest variation in

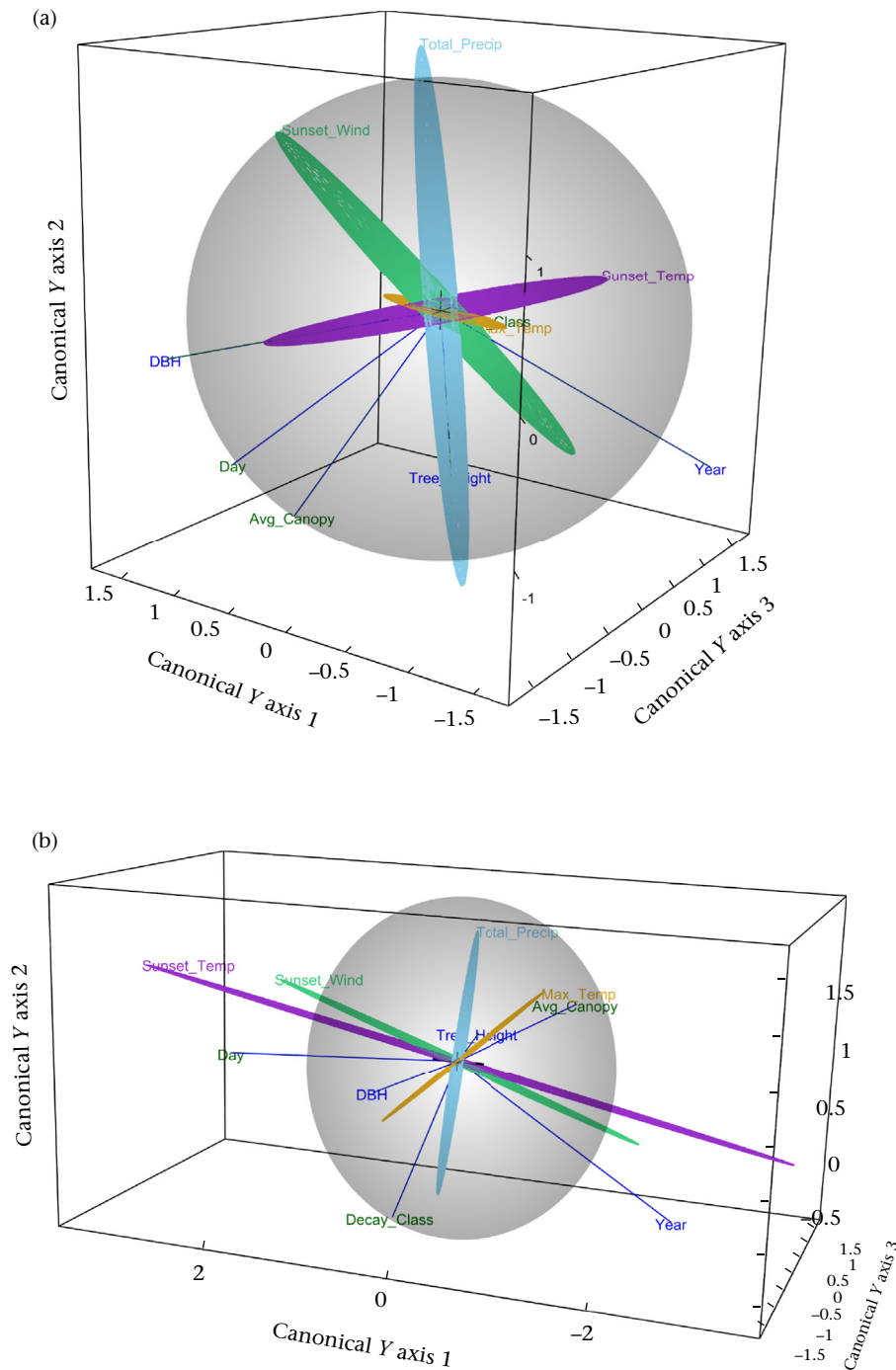


Figure 2. HE plots summarizing canonical correlation coefficients for ambient conditions and roost characteristics of roosts used by female northern long-eared bats, *Myotis septentrionalis*, at (a) Dollar Lake Provincial Park, NS, Canada, from 2005 to 2007, and (b) Fort Knox Military Reservation, KY, U.S.A., from 2011 to 2012. Variables extending beyond the error ellipse (grey) were significant. Coloured ellipses represent effect size of ambient conditions on roost use. Straight lines represent effect size of roost characteristics on roost use. Proximity of ambient conditions and roost characteristics illustrate the strength of relationship between these two variables.

these patterns existed with reproductive condition. Indeed, consistent with other studies, females switched roosts most frequently after weaning, perhaps because they did not face the costs of transporting nonvolant young or returning to roosts at night to nurse young (Ngamprasertwong et al., 2014; Patriquin & Ratcliffe, 2016; Russo et al., 2005).

The effect of ambient conditions on roost switching was the focus of our study, yet the uncertainty in model selection, together with evidence from other studies, suggests there are other

nonmutually exclusive hypotheses that may also explain frequent roost switching. For instance, roost switching may reflect low roost permanence (Lewis, 1995), as bats typically switch among roost trees more frequently than among more permanent roosts, such as caves and artificial structures (Lewis, 1995; Trousdale et al., 2008). Females, however, revisited a number of the same roosts within and between summers in Nova Scotia and Kentucky and they roosted in long-lived tree species and durable snags, suggesting they use relatively permanent roosts but switch, at least in part, to

minimize any mismatch between conditions inside and outside the roosts. Moreover, bats occupying buildings occasionally switch roosts despite warmer temperatures, suggesting thermoregulation is not the only factor influencing roost switching (e.g. Ngamprasertwong et al., 2014). Females may also switch roosts to minimize the risk of predation and transmission of disease and parasites, and to extend their social network and thus facilitate information transfer (Barclay & Kurta, 2007; Bartonička & Růžicková, 2013; Kashima, Ohtsuki, & Satake, 2013; Kerth & Reckardt, 2003; Lewis, 1995; Wilkinson, 1992). Indeed, observations that females found roosting together on one day switched on different days and moved to different roosts (Patriquin et al., 2010; Silvis et al., 2014) suggests that roost switching is not driven solely by changes in ambient conditions and roost characteristics. Alternatively, the roost characteristics we measured may simply not accurately capture the relationship between ambient conditions and roost selection by female northern long-eared bats. Roost characteristics are typically measured as a proxy for cavity properties, which are more likely to influence thermoregulation by bats. However, a recent study demonstrated that external roost characteristics may not reflect cavity structure (Silvis, Thomas, Ford, Britzke, & Friedrich, 2015). In addition, group size may have also played a role in the likelihood of roost switching through its influence on pathogen transmission and thermoregulation (Patriquin & Ratcliffe, 2016). Unfortunately we could not reliably measure group size in our study.

Our findings may help provide some insight into the proximate explanations for frequent roost switching and ultimately the variation in group size and composition characteristic of fission–fusion dynamics documented for northern long-eared bats (Garroway & Broders, 2007; Patriquin et al., 2010) and other temperate bats. Although roost use and roost switching vary across species, roost type (e.g. foliage, tree cavity, cave or building) and region (e.g. Clement & Castleberry, 2013), several studies to date have demonstrated that frequent roost switching, together with variable group size and composition during switches, produce patterns consistent with fission–fusion dynamics (reviewed in Johnson, Ford et al., 2012; Kerth, 2008; Patriquin et al., 2010; Popa-Lisseanu et al., 2008). Although a variety of factors likely contribute to roost switching, it has long been assumed that females switch roosts in response to changes in ambient conditions. Our results support the hypothesis that roost switching by female bats is at least partly explained by changing ambient conditions. However, evidence that bats in different parts of their range respond to different conditions raises the question whether differences in social structure also exist. For example, if conditions are less variable in some parts of their range, do females exhibit more cohesive networks? Accordingly, future work should concentrate on constructing and comparing social networks for northern long-eared bats in each location using the same network metrics. Although social networks have been constructed for northern long-eared bats in Nova Scotia (Garroway & Broders, 2007; Patriquin et al., 2010) and Kentucky (Silvis et al., 2014), each study used different metrics, precluding our ability to compare them here.

Our findings also have potential management implications. Female northern long-eared bats appear to require a network of trees to accommodate changing thermoregulatory demands associated with changes in ambient conditions and reproductive condition. Therefore, conserving trees with ‘average’ characteristics likely will not provide adequate roost habitat for bats, which lends support to previous arguments that multiple roosts should be conserved. For instance, other studies have highlighted the importance of conserving different types of trees to accommodate changes with reproductive condition (e.g. Garroway & Broders, 2008), and our results suggest individual needs vary on a much

finer scale. Therefore, a habitat mosaic consisting of landscape- and stand-level heterogeneity with respect to tree type and age, as well as forest cover, should be maintained to provide a network of suitable roosts (Ethier & Farig, 2010; Silvis, Ford et al., 2015; Silvis et al., 2014).

Moreover, our results suggest that roost switching and roost use vary geographically, presumably in response to differences in climate. Not only does this suggest conservation efforts should be tailored by region (Lacki et al., 2010), but they could also have implications for future management practices in response to climate change. As northern regions continue to become warmer, female northern long-eared bats may require roosts that allow them to minimize overheating on hot days, whereas females at more southern latitudes may increasingly rely on roosts that allow them to minimize overheating. Indeed evidence that differences in roost use between years correlate with differences in temperature suggest that northern long-eared bats are flexible in their roost use and may therefore be resilient to changes in ambient conditions (Silvis, Ford et al., 2015).

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2016.09.022>.

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