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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.

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, & Ibánez, 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, & Garroway, 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 & Růžičková, 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, Piertney, 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.