Appendix H – Literature Review of Habitat Overlap and Competition among *Myotis* and *Perimyotis* Bats
HABITAT OVERLAP AND POTENTIAL FOR COMPETITION AMONG MYOTIS AND PERIMYOTIS BATS

Executive Summary

- Resource Equivalency Analysis (REA) Models may be used in Habitat Conservation Plans (HCP) to determine mitigation needs associated with permitted take.
- The REA Models currently available have been developed by U.S. Fish and Wildlife Service (USFWS 2016) and determine the number of acres needed to potentially offset a number of taken/lost individuals.
- The USFWS has suggested that mitigation credits for any given parcel of habitat should be reduced for one species due to the potential for competitive exclusion by another species.
- Although there is noted overlap in the roosting and foraging behavior of Myotis bat species, there is no empirical evidence of competitive exclusion or displacement of a Myotis or Perimyotis species by another.
- Evidence demonstrates that Myotis and Perimyotis species are able to coexist in the same areas and habitat and at healthy and stable population levels over time.

Introduction

Competitive exclusion is defined as “the exclusion of one species by another when they compete for a common resource that is in limited supply” (Lincoln et al. 2001). For bats, the common resources for co-occurring species are roosts, food, and water. Given that water is not a limited resource in the Midwest, this white paper focuses on summarizing the existing literature with regard to competition in bat communities for roosts and food.

MidAmerican is unaware of any studies that have simultaneously evaluated resource competition for the four species of bats being considered for inclusion in our Habitat Conservation Plan, although several studies have investigated competition between two of the species, and many more studies have investigated competition for limited resources among bat communities. Evidence from available studies demonstrates that co-occurring insectivorous bats have differentiated in ways that result in resource allocation; data do not support roost or foraging competition as an influence on bat community structure (Findley 1993). These studies therefore indicate that there does not appear to be competitive exclusion for the resource(s) investigated.

ROOSTING ECOLOGY

Roost preferences

Extensive empirical evidence has demonstrated that there are biologically significant differences among the roosting niches of Myotis species of bats and of Perimyotis (Foster and Kurta 1999, Carter and Feldhamer 2005, Lacki et al. 2009, Timpone et al. 2010), However, FIndley (1993), looking across a wide variety of bat communities, found no evidence that roost competition has structured any local bat community. At a gross scale, the four species under consideration here utilize resources in fundamentally different ways. For example, northern long-eared bats (NLEB; Myotis septentrionalis) and Indiana bats (INBA; Myotis sodalis) tend to roost in and on the boles
of live and dead trees, whereas little brown bats (LBBA; *Myotis lucifugus*) have adapted to anthropogenic structures and tri-colored bats (TCBA; *Perimyotis subflavus*) roost almost exclusively in the foliage of trees. While NLEB and INBA appear to have similar roosting preferences, they differ in their preferences for location within forest stands and in the roost type, with INBA tending to roost under sloughing and exfoliating or peeling bark in forest interior and NLEB roosting more often in cracks and crevices within the bole, and near forest edges.

Northern long-eared bats are habitat specialists but roost generalists, using a much broader array of roost characteristics, roost types (e.g. cavities, crevices, exfoliating bark) and tree species than INBA (Carter and Feldhamer 2005, Lacki et al. 2009). Unlike INBA, NLEB make extensive use of tree cavities and crevices (Foster and Kurta 1999, Carter and Feldhamer 2005, Lacki et al. 2009, Timpone et al. 2010) in addition to exfoliating bark. In a meta-analysis of NLEB and INBA roost characteristics, Lacki et al. (2009) found that NLEB used cavities and crevices more often, roosted in trees with smaller diameters, and exhibited more variability in roost height and roost DBH than INBA. Several studies have shown that NLEB use live trees more often than INBA (Sasse and Perkins 1996, Foster and Kurta 1999, Carter and Feldhamer 2005, Timpone et al. 2010). Finally, NLEB use roosts with greater canopy cover than INBA, typically requiring 56-84% canopy cover around roosts (Sasse and Perkins 1996, Foster and Kurta 1999, Lacki and Schwierzjohann 2001, Timpone et al. 2010).

Indiana bats tend toward more specific roost preferences and are known to roost almost exclusively under the exfoliating bark of snags and live trees (Kurta and Kennedy 2002, Carter and Feldhamer 2005, USFWS 2007). Females INBA usually select roosts in dead or dying trees (Timpone et al. 2010, Foster and Kurta 1999). When INBA use live trees, they are typically species with characteristic exfoliating bark, such as the shagbark hickories (*Carya ovata*; Gardner et al. 1991, Humphrey et al. 1977, Timpone et al. 2010). Indiana bats prefer trees with less canopy cover and a relatively high amount of solar exposure (USFWS 2007). For example, INBA in Michigan were found to require less than 20% canopy cover at roosts (Foster and Kurta 1999). The USFWS (2007) compiled numerous studies and found INBA prefer ash (Fraxinus spp. 87%) when available, followed by elm (*Ulmus*; 13%), hickory (*Carya*; 22%), maple (*Acer*; 15%), poplar (*Populus*; 9%), and oak (*Quercus*; 15%); regularly use conifer snags in Appalachia (Harvey 2002, Britzke et al. 2003); and rarely use common tree species like beech (*Fagus* spp.), basswood (*Tilia americana*), black cherry (*Prunus serotina*), box elder (*Acer negundo*), or willows (*Salix* spp.). By contrast, Sasse and Pekins (1996) and Silvis et al. (2012) found that NLEB preferred beech, yellow birch (*Betula alleghaniensis*), and sassafras (*Sassafras albidum*). No study to date has demonstrated similar preferences for these tree species in INBA (USFWS 2007). Tri-colored bats prefer oak (*Quercus*), followed by maple (*Acer*), and also used eastern cottonwood (*Populus deltoids*), tulip poplar (*Liriodendron tulipifera*), hackberry (*Celtis occidentalis*), black tupelo (*Nyssa sylvatica*), and elm (*Ulmus*; Veilleux et al. 2003, Leput 2004, Perry and Thill 2007) and dead needles of live short leaf pine (*Pinus echinata*; Perry and Thill 2007).

Little brown bats commonly form maternity colonies in human-built structures including attics, basements, beneath sheet metal roofs, in barn rafters, and in bat houses (Youngman 1975, Davis and Hitchcock 1965, Tuttle 1974) although they will also use hollow trees, natural crevices, and hollows if temperature conditions are right (Barclay 1982). The largest little brown bat maternity
colony ever discovered, numbered 6,700 individuals, and was located in an abandoned barn in Indiana (Whitaker and Hamilton 1998).

Tri-colored bats have little or no competition for roost structures with *Myotis* bats because tri-colored bat roost almost exclusively in foliage, though anthropogenic roosts are also known (Winchell and Kunz 1996, Whitaker 1998). In Indiana, tri-colored bats were found to roost in dead leaves (65%), live foliage (30%), or squirrel nests (5%; Veilleux et al. 2003). Tri-colored bats prefer oak trees (more commonly found in upland mature forests) and roosts near water or perennial streams (Leput 2004), and avoid roosting near forest and field edges (Veilleux et al. 2003) or roads (Perry et al. 2008).

**FORAGING ECOLOGY**

Most insectivorous bats opportunistically prey on insect concentrations when and wherever they occur, as opposed to being dietary specialists (Fenton and Morris 1976), however, the diets of different bat species have been shown to differ and may have evolved in response to foraging competition on the landscape (Findley 1993). For example, selection or preference for particular prey types may be seen where species that are ecologically similar co-occur (sympatry). For example, Husar (1976) found that the southwestern Myotis (*Myotis auriculus*) and the western long-eared Myotis (*Myotis evotis*), two ecologically similar species in New Mexico, had similar diets where they occurred without the other species, with both species feeding on moths and beetles in equal proportion. However, where they occurred in sympathy, the southwestern Myotis fed in greater frequency on moths whereas the long-eared Myotis preferred beetles.

**Diet**

Temperate zone insectivorous bats are generally considered to be generalists and opportunists with regard to the types of insects consumed, as various studies have shown that the orders of insects consumed by one species to be broad and overlapping with other species of bats. Given that aerially active insect prey likely represents an un-defendable resource for bats (Barclay 1991) it is not surprising that available evidence that bats partition prey resources in ways that avoid intraspecific competition. Resource partitioning is thought to arise through differences in timing of foraging, differences in prey consumed (Husar 1976) difference in foraging styles, differences in foraging locations and other behavioral and morphological differences (e.g., Barclay and Brigham 1994). In addition, insectivorous bat echolocation is highly plastic, which allows changes that reduce jamming and interference in the presence of conspecifics or other species (e.g., Faure and Barclay 1994, Obrist 1995). Examples of resource partitioning that avoids direct competition include two species of Myotis bats in the western United States (Husar 1976) and two old-world Myotids (Arlettaz 1999).

In one study, NLEB, LBBA, and INBA consumed the same 10 insect orders although preferences varied (Lee and McCracken 2004). Northern long-eared bats primarily consume beetles, followed by moths, dipterans, and hymenopterans (Lee and McCracken 2004) and also consume orthopterans and arachnids (related to their gleaning ability).
Indiana bats primarily consume moths, then beetles and caddisflies (Brack and LaVal 1985, Kurta and Whitaker 1998, Lee and McCracken 2004). Northern long-eared bats showed a preference for larger species and also ate more arachnids (Lee and McCracken 2004, Feldhamer et al. 2009).

Little brown bats are considered a foraging generalist because they are diverse in their diet and will consume all available insects 3-10 mm in body length (Anthony and Kunz 1977, Feldhamer et al. 2009). Although little brown bats primarily consumed the same 10 insect orders as NLEB and INBA, they have shown a feeding preference for beetles, followed by mayflies (Brack and LaVal 1985, Kurta and Whitaker 1998; Lee and McCracken 2004). Little brown bats were traditionally believed to be an obligate aerial-hawking species, but Ratcliffe and Dawson (2003) demonstrated that they are capable of gleaning moths from bark.

Tri-colored bats are generalist insectivores and will eat leaf hoppers, small beetles, wasps, flies, and moths (Fujita and Kunz 1984). Tri-colored bats preferred leaf hoppers (Cicadellidae), followed by ground beetles (Carabidae), unidentified flies (Diptera), unidentified beetles (Coleoptera), and then moths (Lepidoptera; Whitaker 1972).

**Foraging behavior**

There is no evidence of direct foraging competition between these sympatric bat species. These species often forage at different heights (Humphrey et al. 1977, LaVal et al. 1977, Nagorsen and Brigham 1993) and most importantly, are regularly captured in the same mist-nets at the same sites in multiple years (Whitaker et al. 2004, Hale 2013), indicating that the bats continue to coexist by exploiting resources in slightly different ways. For example, Lee and McCracken (2004) found time of capture of little brown bats was significantly earlier than those of Indiana bats, who in turn were caught earlier than northern long-eared bats when captured at the same site. Moths are typically more abundant later in the night than beetles, flies, and true bugs (which peak at dusk; Anthony and Kunz 1977; Rydell 1992), and this may explain why the two species favoring moths (Lee and McCracken 2004) forage later in the night than little brown bats, who prefer earlier emerging insect species.

Northern long-eared bats use a variety of foraging areas such as interior forest, riparian forest, forested ponds, but are usually closely associated with forest interior (Henderson and Broders 2008). Two acoustic studies found that NLEB detections were associated with high canopy cover (Ford et al. 2005, Yates and Muzika 2006). Northern long-eared bats prefer to forage near ephemeral upland pools (Brooks and Ford 2005, Owen et al. 2003), above and below forest canopy, and within forest clearings (Amelon and Burhans 2006). Northern long-eared bats employ aerial hawking to catch flying insects (Ratcliffe and Dawson 2003, Whitaker 2004) and regularly glean insect prey from the surface of objects (Faure et al. 1993). Typical foraging height of NLEB is 1-3 meters above the ground (LaVal et al. 1977, Nagorsen and Brigham 1993)

Indiana bats forage in a variety of forested features, but are considered riparian forest specialists and more closely linked to riparian areas than NLEB. Indiana bats forage above woodlands and surrounding fields and are also known to forage below forest canopy and within forest clearings (Gardner et al. 1991). Two acoustic studies (Ford et al. 2005, Yates and Muzika 2006) found that Indiana bat detections were associated with high canopy cover, riparian areas, habitat
heterogeneity, and roost availability. Indiana bats typically forage 2 to 30 m (6 to 100 feet) above the ground (Humphrey et al. 1977, LaVal et al. 1977). Indiana bats do not tolerate as much understory vegetative clutter as northern long-eared bats do, preferring instead to forage in areas with low understory vegetative density (Foster and Kurta 1999, Sparks et al. 2005). Sparks et al. (2005) found that Indiana bats use a variety of habitats while foraging and commuting, but appeared to prefer wooded areas.

The foraging niches of NLEB and INBA overlap but there is differentiation between species. The NLEB is an interior forest specialist that stays closer to forest features than Indiana bats (Henderson and Broders 2008). Indiana bats specialize on hydric habitats (Carter 2006) and will forage in open areas and further away from forest features than NLEB (Sparks et al. 2005, USFWS 2007). The diets of the two species can be very similar, but NLEB glean insects and consume Orthopterans and Arachnids on a regular basis unlike Indiana bats. Typical foraging height of the two species is different as well (USFWS 2014). There is currently little available evidence to evaluate whether foraging competition has a significant impact on either species. However, current understanding indicates that the foraging preferences of these two species have diverged to such an extent as to make competition unlikely.

Little brown bats also prefer to forage near water, over open water, grassland, herbaceous, or agricultural habitat along forest edge, or near shorelines (Fenton and Barclay 1980, Nelson and Gillam 2016) and frequently forage with other bat species. This species uses edge and open agricultural fields more often than northern long-eared bats. In Alberta, little brown bats preferentially foraged in forest clear cuts when northern long-eared bats preferred intact interior forest (Patriquin and Barclay 2003). Little brown bats typically forage within 2.1 m (6.9 ft) over the water within 3.2 m (10.5 ft) of the shoreline (Kurta 1982).

Tri-colored bats emerge early in the evening and forage slowly along tree tops, along forest perimeters, over riparian areas and streams, preferring forest or water edge while avoiding interior forest clutter (Nowack 1994, Menzel et al. 2005, Fujita and Kunz 1984).

**CONCLUSIONS**

Empirical evidence shows that the Covered Bat Species – INBA, NLEB, LBBA and TCBA – overlap on the landscape in terms of mist-netting captures and acoustic detections, but that each specializes in their foraging strategy, dietary preference, and roost niche in ways that prevent foraging or roost competition. Forest vegetation patches that are suitable for any one of the four species also contain habitat characteristics and features that are suitable for the other species. This provides the basis for stacking mitigation credit for all four of the Covered Bat Species.
LITERATURE CITED


Leput, D.W. 2004. Eastern red bat (Lasiurus borealis) and eastern pipistrelle (Pipistrellus subflavus) maternal roost selection: implications for forest management. A thesis presented to the graduate school of Clemson University. Available online at: https://www.fs.fed.us/ffs/docs/FFS50abs.pdf


