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Functional significance of emergence timing in bats

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We investigated intraspecific differences in evening emergence time of northern bats *Eptesicus nilssonii*, greater horseshoe bats *Rhinolophus ferrumequinum* and lesser horseshoe bats *R. hipposideros*. Significant differences in emergence time were associated with presumed variation in predation risk, related to light intensity, and energetic benefits of early emergence, caused by differences in age, reproductive state (energetic demands), and body condition. Females of both species emerged progressively later as pregnancy advanced, perhaps because of decreased flight performance, and earlier as lactation proceeded, probably because of increased energy demands and low reserves. Bats under energetic stress, due to persistent low ambient temperatures during pregnancy, or when body reserves were low, emerged relatively early, and hence appeared to take higher risks, than other bats. Young bats emerged much later than the adults at first, but progressively earlier as their flight skills improved. Lesser horseshoe bats emerged later at exposed roost exits than in more protected situations. The results largely corroborate the hypothesis that emergence time, and therefore feeding performance, of insectivorous bats is constrained at bright light conditions, possibly by predation risk (from birds), and modified by energetic considerations.

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Despite a great diversity in food habits and behaviour and a nearly world-wide distribution, bats are virtually exclusively nocturnal, a pattern that seems to be related to increased predation on bats flying in daytime (Speakman 1991, 1995, Fenton et al. 1994). Nocturnality probably evolved because of constraints associated with the use of ultrasonic echolocation. High frequency sound is generally directional and operates only over short ranges (Fenton et al. 1995), largely because of atmospheric attenuation (Lawrence and Simmons 1982). Echolocation in air therefore requires low body mass, which is necessary for slow and manoeuvrable flight (Norberg and Rayner 1987, Barclay and Brigham 1991), and slow flight may in turn be incompatible with efficient avoidance of raptorial birds (Rydell and Speakman 1995).

Timing of evening emergence may have critical implications for fitness in bats. Aerial insects show peak abundance around dusk, when most bats are still confined in their day roost (Racey and Swift 1985, Rydell et al. 1996). Emerging late, therefore, results in missed foraging opportunities at a time of peak prey abundance. Alternatively, early emergence increases exposure to raptorial birds, which may still be active, but whose visual acuity declines rapidly with decreasing luminance (Fox et al. 1976). Hence, leaving early permits access to more food but also leads to higher predation risk. Therefore, bats should show an optimum evening emergence time that is a compromise between these conflicting demands.

This hypothesis has been supported in cross-species analyses of emergence times (Jones and Rydell 1994, Rydell et al. 1996). As predicted, relatively large and fast flying species, which presumably are the least vulnerable to raptorial birds, usually emerge much earlier than slower species. The clustering behaviour of bats

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Predation risk has long been recognised as important in shaping behavioural decisions (review by Lima and Dill 1990). We believe that potential predation risk is of prime importance in determining time of evening emergence in echolocating bats, both within (this paper) and across species (Jones and Rydell 1994). We believe that the relative rarity of raptorial attacks on bats simply reflects a strong selection pressure imposed on bats that make mistakes or that are forced to take risks and therefore fly at the wrong time.

These observations have important implications for bat conservation (Rydell et al. 1996). Protective tree cover around bat roost may be essential for predator avoidance as well as possibly increasing food availability. At protected sites, the bats could emerge earlier and thus take advantage of the dusk peak in insect activity, and perhaps also extend their foraging time. Emergence timing may perhaps also be used as a criterion to judge the levels of energetic stress of females in maternity roosts at specific times of year. Once the normal, non-stressed, pattern of emergence timing is established for a given species at a given roost exit, earlier emergences should indicate significant levels of energetic stress experienced by females.

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