

The Impact of Social Interactions on Torpor Use in Hummingbirds

DONALD POWERS

Biology Department, George Fox University, Newberg, Oregon, USA

Abstract. Measurements of metabolic rate and fat deposition were made on a three-species hummingbird guild in southeastern Arizona to determine if the energetic advantage gained by a dominant territorial species (*Lampornis clemenciae*) over subordinate competitors (*Archilochus alexandri* and *Eugenes fulgens*) resulted in less frequent use of torpor. Results showed that *L. clemenciae* was able to store enough fat during the day to avoid nocturnal torpor. Restricted access to food limited fat storage in both competitors, resulting in frequent torpor use. Avoidance of torpor by *L. clemenciae* supports the notion that use of nocturnal torpor by hummingbirds comes with a cost, and that the ability to avoid torpor is an important benefit to dominant species.

Introduction

Social interactions between hummingbirds are largely shaped by energetic constraints. Territorial species that defend food resources for their exclusive use do so because the energetic benefit exceeds the energetic cost of territorial defense (Kodric-Brown and Brown, 1978). Conversely, nonterritorial species must balance their energy budgets in the face of higher foraging costs due to active exclusion by territory owners or to the use of poor-quality energy resources (Pimm, 1978). Yet in many hummingbird guilds subordinate species seem to thrive, leading one to question whether territorial foraging or dominant status provide a significant energetic advantage as has been assumed (Krebs and Davies 1978). In an assessment of the costs of competition for nectar, Gill (1978) noted that he was “increasingly impressed with the subtlety of behavioral alternatives used

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daily by nectar-feeding birds to maintain a state of energy balance.” In fact Sandlin (2000) showed that the use of “complete information” about a food source by a competitor can lead to foraging strategies that reduce the effects of competition.

The actual energetic success of a nonterritorial competitor hummingbird species is in reality hard to measure because individuals are not easily tracked. This inability to track nonterritorial individuals makes it difficult perform the standard time/energy budget studies associated with cost/benefit analysis. Even in cases where total daily energy expenditure of competitor species have been measured using techniques such as doubly labeled water (Powers and Conley, 1994), the inability to partition energy expenditure into specific activity categories complicates our ability to understand energy management by these species.

One way to compare the energetic state of dominant territorial and subordinate competitor species is to examine their tendency to use nocturnal torpor. For hummingbirds the ability to enter torpor is a protection against an “energy emergency” in which daily energy intake is not adequate to meet energy demands (Hainsworth et al., 1977). Hiebert (1992) showed that an “energy emergency” occurred, and torpor initiated by nonmigratory hummingbirds, whenever energy stores dropped below a set threshold level. Previous studies showing torpor use by hummingbirds experiencing thermoregulatory extremes (e.g., Carpenter, 1974) are consistent with this scenario. With these studies in mind I hypothesized that if territorial hummingbirds have an energetic advantage over competitor species, then they would have less need for torpor and use it less frequently.

Inherent in the suggestion that territorial hummingbirds use torpor less frequently than their competitors is the notion that use of torpor has costs and should be avoided if possible. While several studies have suggested potential ecological and physiological costs for the use of torpor by hummingbirds (Calder III and Booser, 1973; Hainsworth et al., 1977; Hiebert, 1990; Hiebert, 1992), no real experimental validation for these potential costs exist. In the following pages I will make further suggestions for why hummingbirds avoid using torpor and will provide evidence that territorial species gain a competitive advantage by being able to maintain normothermy at night.

Study Site and Species

The studies used in this analysis involved a three-species hummingbird guild located in the Chiricahua Mountains of southeastern Arizona. Details of both the

study area and species have been published elsewhere (Pimm et al., 1985; Powers and Conley, 1994; Sandlin, 2000a, 2000b). This system is ideally suited for studying the impact of social interactions on torpor use because the hummingbird species comprising the guild exhibit distinctly different foraging modes and represent a gradient within their dominance hierarchy. The blue-throated hummingbird (*Lampornis clemenciae*; 8.0 g) is an aggressive, dominant species that exhibits classical territorial behavior that results in the exclusion of potential competitors from its food source. The main competitors in this system are the black-chinned hummingbird (*Archilocus alexandri*; 3.5 g) and the magnificent hummingbird (*Eugenes fulgens*; 7.5 g). *Archilocus alexandri* is a primary competitor that acquires most of its energy by intruding on *L. clemenciae* territories. *Eugenes fulgens* is also subordinate to *L. clemenciae*, but uses a trapline foraging strategy (Powers, 1996) that allows it to avoid frequent interaction with *L. clemenciae* (Sandlin, 2000b).

Methods Summary

Hummingbirds were trapped at dusk so that their fat stores were a result of normal daytime activity. Prior to metabolic measurements, birds were fed (except where noted) to simulate the pre-roost meal that is likely part of a hummingbird's nightly routine (Calder III et al., 1990). Nighttime metabolism was measured under temperature conditions that closely approximated the natural environment using open-flow respirometry. Total body fat was measured prior to roosting, at the onset of torpor, or at the end of nighttime (for birds that remained normothermic) using solvent fat extraction. Total body fat at the onset of torpor was assumed to be the torpor threshold. Details of these methods can be found in Powers et al., 2003.

Fat Storage in Territorial vs. Competitor Species

Fat storage data for all species when feeding primarily from feeders containing an energy-rich 1 M sucrose solution (35% sucrose; Baker, 1975) are summarized in Fig. 1. Under these conditions *L. clemenciae* stored significantly more fat during the day than either competitor species, indicating that territoriality did result in an energetic advantage. This energetic advantage was substantial in that total body fat for *L. clemenciae* amounted to twice the measured torpor threshold for body fat in these species (ca. 4% of body mass; Powers et al., 2003), whereas total body fat in both competitors was only slightly above threshold. The high variability in total body fat observed in *E. fulgens* probably corresponds to vari-

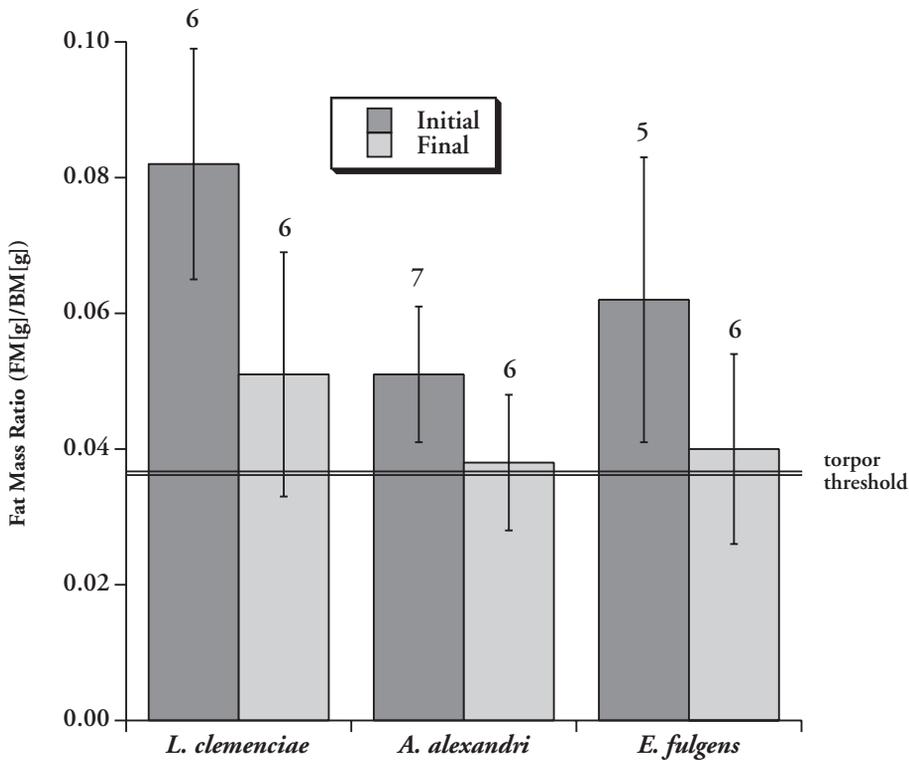


Fig. 1. Ratio of total body fat to wet mass for each study species when fed energy-rich sucrose solution. Data are presented as mean \pm SD. Numbers above error bars are sample sizes. Both initial (pre-roost) and final (onset of torpor or end of night) total body fat in *L. clemenciae* was significantly higher than in the other species.

ability in daily energy intake related to their trapline-foraging behavior. The extra energy stored by *L. clemenciae* more than compensates for the high cost of territorial defense and a daily energy expenditure that exceeds their predicted expenditure by 87% (Powers and Conley, 1994).

Fat storage data for *L. clemenciae* when feeding primarily from feeders containing an energy-poor 0.5 M sucrose solution (17% sucrose) are summarized in Fig. 2. Total body fat was only 72% of that previously measured when energy-rich sucrose solution was used, whereas fat storage in both competitor species was unchanged. Possibly, *L. clemenciae* was unable to increase foraging to compensate for the reduction in energy content of their food due to time

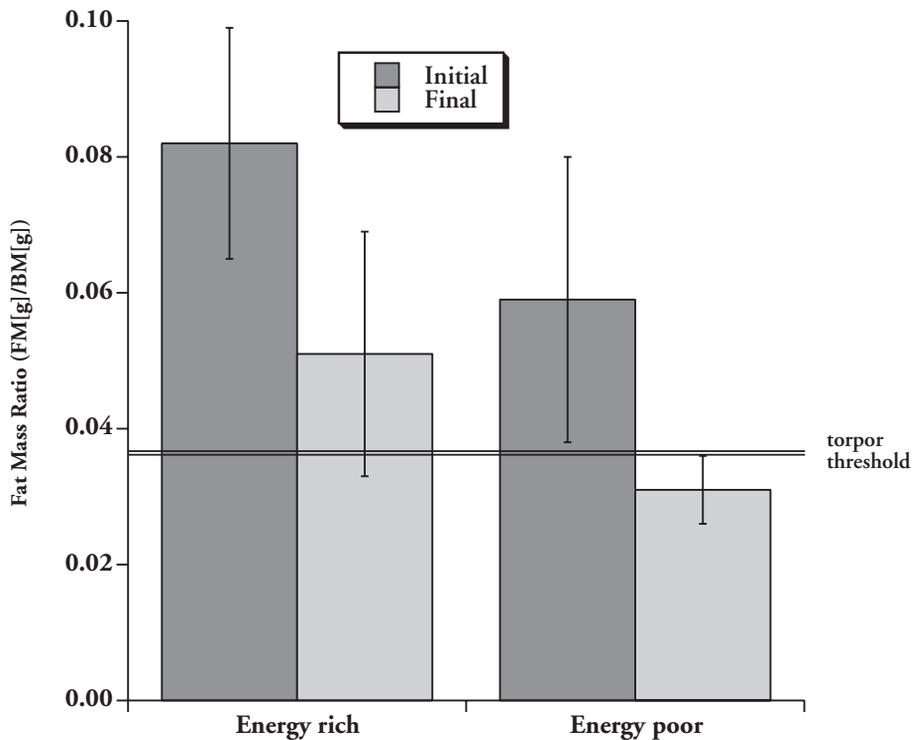


Fig. 2. Ratio of total body fat to wet mass for *L. clemenciae* when fed energy-rich vs. energy-poor sucrose solution. Initial total body fat was lower and final total body fat fell below threshold when the energy-poor sucrose solution was used. In all cases $n = 6$.

requirements for territorial defense or to physiological limits on the ability to process nectar (McWhorter and Martinez del Rio, 1999). In any event, in the face of lower energy rewards, the benefit of being territorial was reduced as has been previously suggested (Kodric-Brown and Brown, 1978).

Relationship Between Torpor Use and Fat Storage

In all species, initial total body fat was significantly greater than final body fat, indicating that fat was catabolized to meet nighttime energy demands. Total body fat in both competitors frequently reached the threshold level at night, causing torpor. The use of torpor by all species is summarized in Fig. 3.

Nearly all *A. alexandri*, who foraged primarily by robbing nectar from *L. clemenciae* territories, used torpor. In this system use of torpor is probably the

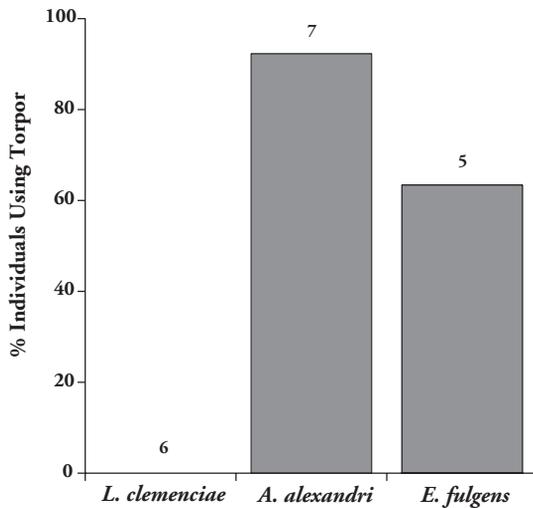


Fig. 3. Percent individuals from each study species using torpor when fed energy-rich sucrose solution.

only way this small, classical competitor can remain in energy balance in light of their low fat storage. Fat storage by *A. alexandri* was not reduced solely by the high energetic cost of being small, but also by competition with *L. clemenciae*. This is supported by the fact that mass-specific daily energy expenditure by *L. clemenciae* is 15% higher than in *A. alexandri*, and that the larger *E. fulgens* also had low fat storage. It would be interesting to look at *A. alexandri* in other systems where they frequently adopt territorial behavior (e.g., Copenhaver and Ewald, 1980), to determine if territoriality would provide sufficient energy to permit nighttime normothermy in spite of the higher metabolic costs associated with small body size.

Lower torpor use and more variable fat storage by *E. fulgens* indicate that for this species traplining has the potential for energy rewards higher than that experienced by *A. alexandri*, but that actual energy intake is unpredictable. Higher energy reward is likely due to their not being constrained by territorial behavior like *A. alexandri* (Sandlin, 2000b), and possible supplementation of their diet with arthropods at a level higher than that which occurs in most hummingbirds (Van Hook et al., unpublished). The end result is that nighttime normothermy can be maintained about 36% of the time.

Final total body fat in *L. clemenciae* reached the torpor threshold prior to the end of night only when feeders contained the energy-poor solution, which was the only time when *L. clemenciae* used torpor (two of six entered torpor). The

fact that no *L. clemenciae* entered torpor when energy was abundant, and only 33% entered torpor when energy availability was reduced, supports the notion that torpor was avoided when energy storage could fuel nighttime normothermy.

Importance of Crop Energy to Nighttime Metabolism and Torpor

Broad-tailed hummingbirds (*Selasphorus platycercus*) engage in hyperphagia to energy load their crop 20 minutes prior to going to roost (Calder III et al., 1990). Is this energy an important supplement to nighttime metabolism? Calder III et al. (1990) showed that *S. platycercus* filled their crops to 179% of predicted volume and suggested that the energy stored was sufficient to support nighttime normothermy without fat catabolism. The use of pre-roost hyperphagia by other hummingbirds has not been studied. Bech et al. (1997) found that a “significant fasting period” (20–100 minutes) was required in two of three species they studied in order to induce torpor. In these species the loss of crop energy may have played some role in the increased incidence of torpor after fasting.

The role crop energy plays in supporting nighttime metabolism was examined in *L. clemenciae* and *A. alexandri* by measuring torpor use in birds denied a pre-roost meal (Powers et al., unpublished; Fig. 4). Torpor use pattern differed only in *L. clemenciae* where the loss of crop energy caused all individuals to use torpor. This use of torpor suggests that in this system dominance and territoriality is not sufficient to support nighttime normothermy exclusively with fat stores.

The most striking result of these experiments was the inability of *A. alexandri* to arouse from torpor. These birds had to be hand warmed and fed at the onset of the active period. If these measurements represent what goes on in wild populations, then the energetic tightrope walked by species like *A. alexandri* becomes narrower, and the importance of their being good competitors amplified (Powers and McKee, 1994; Sandlin, 2000b).

Are There Potential Costs to the Use of Torpor by Hummingbirds?

Because the use of torpor generally results in energetic gain (Hiebert, 1990), the ability of *L. clemenciae* to avoid torpor is advantageous only if the use of torpor has associated costs. The fact that *L. clemenciae* does indeed avoid torpor suggests some benefit to remaining normothermic at night. While several potential costs have been suggested (Hainsworth et al., 1977; Hiebert, 1990; Hiebert,

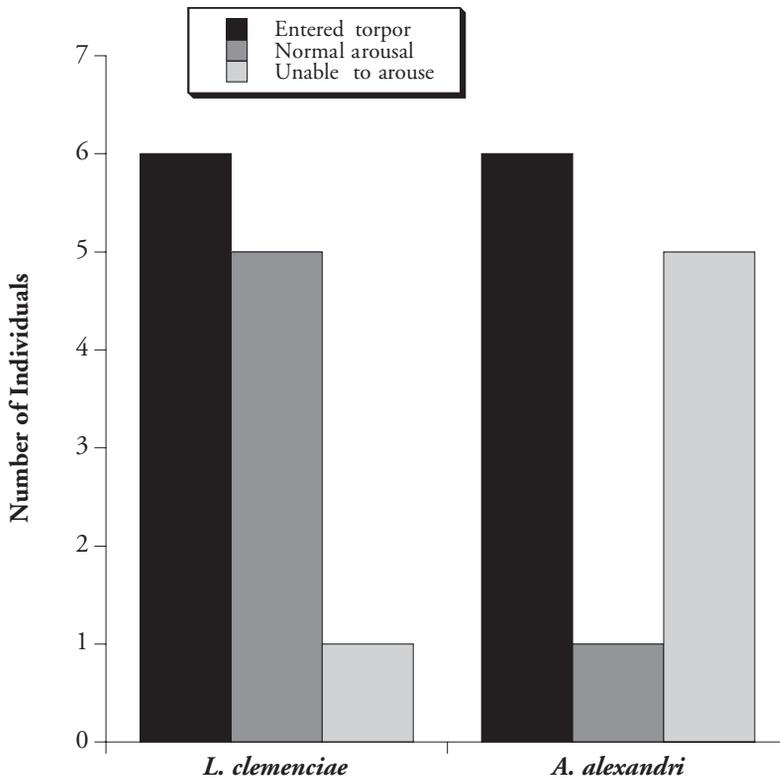


Fig. 4. Number of *L. clemenciae* and *A. alexandri* that used torpor, aroused from torpor normally, and were unable to arouse from torpor when denied a pre-roost meal.

1992), no studies demonstrate that these costs are real. Future studies addressing potential costs of torpor must be done if we are to completely understand the role torpor plays in long-term energy management in hummingbirds.

There are logical reasons why *L. clemenciae* might avoid torpor when they are energetically able. One possibility would be increased risk of predation. There is actually little evidence that adult hummingbirds are a major prey item for any species (Miller and Gass, 1985), and the only information available for the study species is anecdotal at best. However, these hummingbirds likely roost on branches of shrubs or trees, and if they could be located, torpid birds would be unable to escape. There is indication that nocturnal species such as ring-tailed cats (*Bassariscus astutus*) and a variety of arboreal snakes in the study area have to some degree preyed upon hummingbirds (D. Powers, pers. observation). A sec-

ond possible cost is early access to food. At SWRS, *L. clemenciae* typically arrives at feeders about 15 minutes before *A. alexandri* in the morning (D. Powers, pers. observation). While there is no way of knowing if this pattern is related to *A. alexandri*'s regular use of torpor, or perhaps their difficulty in arousing from torpor, the delay in the onset of foraging might put them in the position of having to make up an energy deficit from the very beginning of the day.

Conclusions

Dominant, territorial *L. clemenciae* had a relative body fat content that was twice that measured in its primary competitors, suggesting that an energetic advantage was gained by restricting access to its food source. The higher fat stores of *L. clemenciae* provided sufficient energy to support normothermic nighttime metabolism, whereas both competitor species had to use torpor to balance their energy budget. Energetic constraints were most severe for *A. alexandri*, which needed to use torpor almost every night. The energetic tightrope walked by *A. alexandri* was further evidenced by their inability to arouse from torpor when they entered the nighttime period without energy stored in their crop. The regular use of torpor by both competitor species supports the hypothesis that hummingbirds whose access to energy resources is restricted by social interactions such as territoriality will use torpor more frequently.

Even though the use of torpor results in an energetic savings for hummingbirds, the fact that *L. clemenciae* routinely avoids torpor suggests that torpor has associated costs. If so, then monitoring torpor use in the various hummingbird species in a social group might provide insight into their energetic success. While several potential costs have been proposed both here and elsewhere, none have been experimentally demonstrated for hummingbirds. Before we can fully understand the role torpor plays in the long-term management of hummingbird energetics, studies addressing these potential costs will have to be done.

Acknowledgements

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