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Solar Radiation and the Energetic Cost of Rewarming from Torpor

Andrew E. McKechnie and Blair O. Wolf
Biology Department, MSC03-2020, University of New Mexico, Albuquerque, NM 87131-0001, USA

Abstract. We modeled the effect of basking behavior on the energy required to rewarm from torpor ($E_{\text{rewarm}}$), using solar heat gain data for birds. Our model suggests that reductions in $E_{\text{rewarm}}$ can be considerable (up to ca. 60%), and vary with latitude, season, and time of day. We argue that variation in the effects of solar radiation (SR) on rewarming rate and $E_{\text{rewarm}}$ can be thought of as a continuum from passive to augmented modes of SR-assisted rewarming. Passive rewarming rates are generally lower than endogenous rewarming rates.

Introduction

The energy required to rewarm to normothermic body temperature is a major constraint on the energetic benefits of torpor (Prothero and Jürgens, 1986; McKechnie and Wolf, this volume). Short-wave solar radiation can dramatically affect the energy balance of endotherms, and there has recently been considerable interest in the importance of solar radiation (SR) for ameliorating the energetic cost of rewarming. For example, Mzilikazi et al. (2002) provided indirect evidence that the majority of arousals in free-ranging rock elephant shrews (Elephantulus myurus) were SR-assisted. Geiser et al. (2002) found that fat-tailed antechinus (Pseudantechinus macdonnellensis) bask extensively during rewarming. Less is known from birds, but solar radiation appears to be involved in rewarming from shallow hypothermia in greater roadrunners (Geococcyx californianus), torpor in tawny frogmouths (Podargus strigoides), and hibernation in common


The heat loads experienced by endotherms during exposure to solar radiation depend on numerous factors. Various structural and optical properties of the pelage or plumage interact with properties of the physical environment (irradiance and wind speed) to determine the heat load transferred to the skin (Walsberg, 1983; Wolf and Walsberg, 2000). Hence, it is impossible to model in a simple way the rate of heat transfer during basking behavior. However, laboratory measurements of solar heat gain (SHG), calculated as the reduction in metabolic heat production during exposure to simulated solar radiation (Wolf et al., 2000), can be used to estimate these heat fluxes under natural conditions. We developed a model based on avian SHG data, in order to investigate the potential effects of solar radiation on the energetics of rewarming from torpor.

**Materials and Methods**

To place boundaries on the solar radiation potentially available to endotherms, we calculated annual maximum and minimum levels for various latitudes. We predicted solar irradiance at an altitude of 600 m a.s.l. at various times of the day at various latitudes using equations 11.1 to 11.13 in Campbell and Norman (1998), assuming an atmospheric transmittance of 0.65. We then obtained SHG data collected or estimated for free convective conditions from laboratory studies for white-crowned sparrows (*Zonotrichia leucophrys*; De Jong, 1976; Wolf et al., 2000), greater roadrunners (*Geococcyx californianus*; Ohmart and Lasiewski, 1971), brown-headed cowbirds (*Molothrus ater*), zebra finches (*Taeniopygia guttata*; Lustick, 1969), and white-backed mousebirds (*Colius colius*; Mckechnie, 1998). Because SHG is affected by an animal's orientation, we calculated solar heat gain per unit projected area perpendicular to the irradiance beam ($A_p$). In studies where the orientation of the bird relative to the irradiance source was not specified, we assumed a ratio of $A_p$ to total surface area ($A_p/A$) of 0.24, corresponding to a prolate spheroid with a major axis twice as long as the minor axis, orientated at 60° to the irradiance beam (Campbell and Norman, 1998; Wolf et al., 2000). We used these data to generate an equation relating SHG to irradiance. We then used this equation to estimate SHG from predicted solar irradiance. To estimate the energy savings associated with basking during rewarming from torpor, we integrated predicted SHG and compared it to the estimated energetic cost of rewarming ($E_{rewarm}$) at an air temperature of 0° C and a torpor body temperature setpoint of 18° C (Mckechnie and Wolf, this volume). We
assumed (1) that a bird is exposed to solar irradiance for the entire duration of the rewarming phase, and (2) that rewarming rate during SR-assisted rewarming is identical to that during endogenous (i.e., non-SR-assisted) rewarming. Hence, this model examines only one of several ways in which solar radiation can affect $E_{	ext{rewarm}}$ (see Discussion).

**Results**

Solar irradiance shows considerable variation with time of day, time of year, and latitude. Seasonal variation is small at low latitudes but increases at higher latitudes. At the equator, solar irradiance one hour after sunrise varies from a minimum of 366 W m$^{-2}$ (solstice) to a maximum of 403 W m$^{-2}$ (equinox), and at midday varies from 1,011 W m$^{-2}$ (solstice) to 1,046 W m$^{-2}$ (equinox). At a latitude of 30°, solar irradiance one hour after sunrise varies from 240 W m$^{-2}$ (winter solstice) to 285 W m$^{-2}$ (summer solstice), and at midday varies from 813 W m$^{-2}$ (winter solstice) to 1,043 W m$^{-2}$ (summer solstice). At a latitude of 60°, solar irradiance on the summer solstice is 61 W m$^{-2}$ one hour after sunrise and 955 W m$^{-2}$ at midday, but never increases above 90 W m$^{-2}$ during the 5.4 hour long day on the winter solstice.

The SHG and irradiance data we obtained from the literature were best described by a linear regression forced through the origin, with $\text{SHG} = 0.2055$ irradiance ($r^2 = 0.463$), where SHG and irradiance are in W m$^{-2}$. The fact that a linear regression model provided a better fit than an exponential decay model (De Jong, 1976; Walsberg et al., 1997) probably reflects variation in experimental conditions, such as lamps with different color temperatures, typically well below that of the sun.

Our model predicts that birds save considerable amounts of energy by basking during rewarming from torpor (Fig. 1). Our model also reveals that the energetic benefits of SR-assisted rewarming vary with latitude, season, and body size but also with the time of day when rewarming occurs (Fig. 1). For instance, low irradiance levels early in the day mean that small birds rewarming from torpor immediately following sunrise derive very little benefit from SR-assisted rewarming (Fig. 1). In fact, over most of the body size range we examined, SR-assisted rewarming is more beneficial for species that rewarmin later in the day, since rewarming then coincides with higher irradiance levels (Fig. 1).
Fig. 1. Predicted avian energy savings associated with SR-assisted rewarming from torpor as a function of body mass. The savings are predicted for maximum (left-hand graphs) and minimum (right-hand graphs) annual solar irradiance levels at three latitudes: equator (top graphs), 30° C (center graphs) and 60° C (bottom graphs). In each graph, energy savings are predicted for birds commencing rewarming from torpor at sunrise, midmorning, midday, and midafternoon respectively.
Discussion

Our model predicts that basking behavior substantially reduces energy expenditure during rewarming and suggests that the availability of solar radiation is an important determinant of the energetic benefits of torpor. These predictions are consistent with several recent studies that examined the importance of basking behavior in free-ranging endotherms (Geiser et al., 2002; Mizlikazi et al., 2002; Woods, 2002). Geiser et al. (2002) found that P. macdonnellensis adjust the timing of rewarming to coincide with the availability of solar radiation. On clear days, P. macdonnellensis typically delayed rewarming until 2 hours after sunrise (Geiser et al., 2002). Mammalian data are very similar to those for birds in terms of the percentage of solar irradiance that represents physiologically significant SHG, suggesting that our model’s predictions are applicable to both mammals and birds.

In striped-faced dunnarts (Sminthopsis macroura), $E_{\text{rewarm}}$ during radiant energy-assisted rewarming was reduced by 85% compared to endogenous arousal (Geiser and Drury 2003), a greater reduction than predicted by our model (Fig. 1). These authors used a radiant heat source with a color temperature of 2850° K, substantially lower than that of the sun (5800° K). Animals generally absorb a far greater fraction of intercepted long-wave radiation than short-wave radiation (Walsberg 1983; Wolf and Walsberg 2000). Hence, the large reductions in $E_{\text{rewarm}}$ observed by Geiser and Drury (2003) may in part reflect the fact that compared to the sun, the emission spectrum of their artificial radiation source was shifted towards longer wavelengths.

Solar radiation can affect the energetic cost of rewarming in several ways. At one extreme, endotherms may minimize $E_{\text{rewarm}}$ by allowing solar radiation to passively elevate $T_v$. Passive rewarming will typically involve lower rewarming rates (see below) and lower energy expenditure than endogenous rewarming. At the other extreme, endotherms may minimize the duration of the rewarming phase by augmenting metabolic heat production with solar radiation. Augmented rewarming will involve higher rewarming rates and similar energy expenditure compared to endogenous rewarming. Passive and augmented modes of rewarming represent the ends of a continuum describing the potential effects of solar radiation on the energetic cost of rewarming from torpor. The scenario we have modeled in Figure 1, in which rewarming rates during SR-assisted rewarming remain the same as during endogenous rewarming, represents the midpoint. Mammalian data provide support for the notion of such a continuum. In rock elephant shrews, rewarming rates during SR-assisted rewarming were on
average < 33% of rewarming rates during endogenous rewarming (Mzilikazi et al., 2002), suggesting that rewarming was at least partly passive and hence that $E_{\text{rewarm}}$ was reduced. In contrast, basking fat-tailed antechinus rewarmed twice as fast as nonbasking individuals (Geiser et al., 2002), suggesting augmented rewarming.

Rewarming rate should vary considerably depending on the mode of rewarming (passive SR-assisted, endogenous, or augmented SR-assisted). The theoretical maximum passive rewarming rate will occur when heat loss to the environment is zero, and under these conditions, $R_{\text{pmax}} = \text{SHG}/(sM_b)$, where $R_{\text{pmax}}$ is the maximum passive rewarming rate (°C min⁻¹), SHG is solar heat gain (J min⁻¹), s is the specific heat of animal tissues (3.43 J g⁻¹°C⁻¹), and $M_b$ is body mass (g). Predicted $R_{\text{pmax}}$ is lower than endogenous rewarming rate, except in larger birds ($M_b > 150$ g) at high irradiance levels (Fig. 2). Because $R_{\text{pmax}}$ is a theoretical maximum value possible only under unrealistic conditions of zero environmental heat loss, passive SR-assisted rewarming will almost always be slower than endogenous rewarming. The difference between $R_{\text{pmax}}$ and endogenous rewarming rate increases with decreasing $M_b$ (Fig. 2). Empirical observations support these predictions. Hibernating common poorwills (45 g) in artificially shaded roost sites warmed at an average of 0.39° C min⁻¹, but in sunlit roost sites passive warming occurred at ca. 0.08° C min⁻¹ (Woods, 2002).

One might expect differences in the extent of passive vs. augmented SR-assisted rewarming to be related to the need for energy conservation and to predation risk during rewarming. For instance, an endotherm that experiences a high predation risk might employ augmented SR-assisted rewarming to minimize the duration of the rewarming phase. On the other hand, an endotherm that experiences a low predation risk might employ passive SR-assisted rewarming to minimize $E_{\text{rewarm}}$, particularly in an environment where energy availability is low and/or unpredictable.

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Fig. 2. Predicted avian maximum rewarming rate ($R_{\text{max}}$) during passive SR-assisted rewarming as a function of body mass. The dashed lines indicate $R_{\text{max}}$ for three irradiance levels, covering the range of solar irradiance likely to be experienced by free-ranging endotherms. The solid line indicates predicted endogenous rewarming rates (McKechnie and Wolf; this volume).

References


