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Abstract

Eared Grebes (*Podiceps nigricollis*) encounter a variety of climatic regimes in their annual cycle. The most dramatic occur while on staging areas in autumn. We investigated the thermoregulatory abilities of the Eared Grebe to determine how they coped with these climate changes during staging. The basal metabolic rate (BMR) was higher than predicted. Mass-specific BMR was 1.212 mL O₂/g·h for birds averaging 317 g. The thermoneutral zone is wide and extended from 15°C to 38°C. Minimal thermal conductance and average body temperature were not unusual. We conclude that Eared Grebes live most of the year under thermoneutral conditions and that food availability, not temperature extremes, determines the timing of their winter migration.

Keywords

Eared Grebe, Black-necked Grebe, temperature regulation, BMR, thermal conductance, climate, distribution, *Podiceps nigricollis*

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Temperature Regulation and the Constraints of Climate in the Eared Grebe

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Abstract.—Eared Grebes (*Podiceps nigricollis*) encounter a variety of climatic regimes in their annual cycle. The most dramatic occur while on staging areas in autumn. We investigated the thermoregulatory abilities of the Eared Grebe to determine how they coped with these climate changes during staging. The basal metabolic rate (BMR) was higher than predicted. Mass-specific BMR was 1.212 mL O₂/g·h for birds averaging 317 g. The thermoneutral zone is wide and extended from 15°C to 38°C. Minimal thermal conductance and average body temperature were not unusual. We conclude that Eared Grebes live most of the year under thermoneutral conditions and that food availability, not temperature extremes, determines the timing of their winter migration. *Received 13 July 2002, accepted 6 February 2003.*

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The Eared Grebe (*Podiceps nigricollis*), also called the Black-necked Grebe in Europe and Africa, has a complex life history, migrating into several areas with different and variable climates (Cullen *et al.* 1999). In North America, they breed throughout much of the western interior of the northern United States and southern Canada. They remain on the breeding grounds from mid-spring to late summer, then begin to migrate to staging areas from late July. Two hypersaline areas at similar latitudes and relatively similar altitudes, Mono Lake, California (38°N, 2,100 m) and Great Salt Lake, Utah (41°N, 1,400 m), account for 99% of staging Eared Grebes in North America (Jehl *et al.* 2003). Although the temperature is warm when they arrive, the climate in both regions cools through the autumn and may become cold before they leave. Sometime between mid-November and December, the grebes migrate south, mostly into the Gulf of California, Mexico, where they remain for one or two months before beginning their northward migration. This migration return takes most of them first to the Salton Sea, California, where they remain for several weeks. Following that, they return to their breeding grounds, sometimes visiting Great Salt Lake (Jehl and McKernan 2002; Jehl *et al.* 2003).

Despite their migrations, these birds are flightless most of the year, undergoing rapid atrophy of their breast muscles and existing solely as foot-propelled swimmers and divers for as much as ten months of every year (Jehl 1997; Jehl *et al.* 2003). Consequently, they may be subjected to climate changes from which they cannot rapidly escape. The most dramatic climatic shift occurs on the staging lakes in autumn, where they arrive in the heat of the late summer and remain until early winter. During autumn staging, Eared Grebes show rapid gain of mass, mostly fat. They do not lose mass, even in the coldest weather, until they are ready to migrate. Thermoregulatory abilities of Eared Grebes in the autumn staging lakes protect them from heat stress in late summer and early autumn as well as cold stress at the end of their staging sojourn. We examined their metabolic responses to a variety of temperatures to assess their physiological ability to cope with varying regimes while staging.

METHODS

We used two groups of grebes captured at Mono Lake, California in August-September from 1984 to 1991 and returned to the wild at the end of the study. Members of one group (N = 20) were transported within 24 h to San Diego, California, where they were main-

tained outdoors for several weeks. Metabolic measurements were begun within a week of capture; some birds were measured over a period of as much as ten weeks. Approximately 12-14 h prior to a measurement, they were placed in a holding cage and deprived of food. We made metabolic measurements on a second group (N = 22), captured in August between 1986 and 1991 at Mono Lake after the birds were judged postabsorptive (i.e., deprived of food for ≥ 14 h) and then released them at the lake within 36 h of capture.

Metabolic rates were measured as oxygen consumption in chambers connected in open circuit (Depocas and Hart 1957) to a two-channel Applied Electrochemistry S-3A® oxygen analyzer; oxygen concentration was measured in CO₂-free, dry air. Birds were allowed to equilibrate in a 20 L plexiglass chamber or a 30 L titanium chamber for about an hour before measurements were begun. Measurements continued for a minimum of two hours and until a minimal level of oxygen consumption was reached. Activity of birds in the chamber could be heard or recorded as changes in oxygen consumption; measurements of active birds were not used. Air flow rates ranged from about 1.7 to 3.3 L/h, with higher rates in the larger chamber. All birds were in the dark. Daytime measurements were begun and ended during real time daylight. Nighttime measurements were begun at least one hour after the onset of outdoors darkness and often were conducted for considerably longer times. If a second run was conducted the same night, it typically began after midnight.

Two protocols were used. For all birds measured at Mono Lake and initially for the San Diego birds, flow rates of dry air were measured with Brooks® rotameters calibrated to a 1% error by a 2.0 L SKC® soap film volumeter, and F_{O₂}'s (fraction of oxygen in the airstream) were recorded on an Omniscrite® recorder, then converted to standard conditions using the temperature of air flowing through the rotameter and the barometric pressure during the experiment. In later San Diego experiments, flow rates were measured using Tylan FM 380® mass flow meters; oxygen concentrations (F_{O₂}), flow rates, and chamber temperatures were recorded every 20 s by a computer, following A/D conversion by a MetraByte DAS-8® board and after averaging ten data points for each.

Chamber temperatures were monitored continuously with a copper-constantin thermocouple connected to the DAS-8® via a MetraByte EXP-16® board or with a Yellow Springs Instrument telethermometer with a YSI 401® probe. In San Diego, those chamber temperatures were maintained $\pm 1^\circ\text{C}$ by a Hotpack® refrigerated incubator. Body temperatures (T_b) for metabolic experiments were measured within one minute of termination of an experiment by use of a YSI telethermometer with a YSI 402® small animal probe inserted into the grebe's proventriculus.

All values for thermal conductance come from the San Diego group, where the thermal neutral zone (TNZ) was determined and air temperatures below thermoneutrality could be maintained. Most nighttime measurements on staging birds were made on the Mono Lake group. All values of oxygen consumption are reported as dry gas at standard temperature and pressure (STPD). Conversions of measured O₂ consumption to SI units assume an RQ of 0.71 (King 1957; cf. Ellis and Gabrielsen 2001). For this paper, we define basal metabolic rate (BMR) as the metabolic rate measured in these birds while at rest, in their thermal neutral zone,

and while post-absorptive; there was no circadian effect (see below).

Statistical tests were made with Quattro Pro 8®, Statistica 5®, or SPSS 8®. All our measurements of central tendency and dispersion are means and standard deviations, unless otherwise noted. To prevent pseudoreplication (Hurlbert 1984), all BMR data were averaged for each bird prior to analysis, unless otherwise noted.

RESULTS

Basal metabolic data were pooled after detecting no circadian and group differences. Mass-specific BMR of eight birds measured at night was 10.5% less than that of 32 birds measured in the daytime, but the range fit within the daytime range and was not significantly different. There was also no significant difference between the San Diego and Mono Lake groups. The pooled value for BMR was 385.1 ± 86.6 mL O₂/h (mean mass = 317.4 ± 51.3 g; N = 40), which is 30% higher than predicted by the time-insensitive allometric equation of Lasiewski and Dawson (1967) for a nonpasserine species of its size. Comparisons of BMR with other allometric equations are given in Table 1. Mass-specific BMR was 1.212 ± 0.195 mL O₂/g·h.

Mass-specific metabolism is plotted against air temperature in Fig. 1. In experiments conducted at temperatures from -12.5°C to 38.6°C , the thermoneutral zone (TNZ) ranged from 15.0°C to 38.1°C . One measurement at 1.2°C (1.077 mL O₂/g·h, T_b = 39.7°C) was indistinguishable from BMR.

Like most birds, Eared Grebes maintain body temperature by mixing chemical and physical responses to temperatures below TNZ (Schmidt-Nielsen 1977; McNab 1980). Consequently, they exhibited different values of thermal conductance, which appear as slopes in Fig. 1; the highest and lowest are presented there. Minimal thermal conductance (i.e., a purely chemical or metabolic response to decreasing temperature) is 0.0501 ± 0.0036 mL O₂/g·h·°C (N = 8 experiments on five birds). This is 10% higher than the time-insensitive value predicted by Lasiewski *et al.* (1967) for a nonpasserine bird of this size (309.1 ± 41.2 g, where the small difference in mass from BMR reflects differences in the birds measured). Two measurements on different birds at the lowest

Table 1. Allometric comparisons of basal metabolic rate (BMR) and thermal conductance (TC) of Eared Grebes.

	N ^a	Mass (g)	Measured value ^b	Percentage of predicted values			
				Lasiewski ^c	Aschoff ^d : α	Aschoff ^d : ρ	Reynolds & Lee ^e
BMR	40	317 ± 51.3	1.212 ± 0.1195	129.8	110.8	137.9	129.0
TC	5; 8	309 ± 41.2	0.0502 ± 0.0036	109.7	84.9	149.7	NA

^aNumber of birds: for TC number of birds followed by number of measurements.

^bBMR in mL O₂/g·h; TC in mL O₂/g·h·°C.

^cFor BMR, Lasiewski and Dawson (1967); for TC, Lasiewski *et al.* (1967).

^dFor BMR, Aschoff and Pohl (1970); for TC, Aschoff (1981); α and ρ are the active and resting circadian phases of birds, for grebes daytime and nighttime, respectively.

^eReynolds and Lee (1996).

temperature (-12.5°C) did not indicate an expected low thermal conductance, but both were measured in March during a time of heavy molt, which could have compromised their insulation; these two individuals increased their oxygen consumption by 2.87 × BMR.

Body temperatures (T_b) stayed nearly constant ($39.6 \pm 0.9^\circ\text{C}$). Within the TNZ, daytime and nighttime average T_b were indistinguishable, varying by only 0.05°C. Out of a total of 121 metabolic experiments at different air temperatures, only three values for body temperature exceeded 41.0°C. The

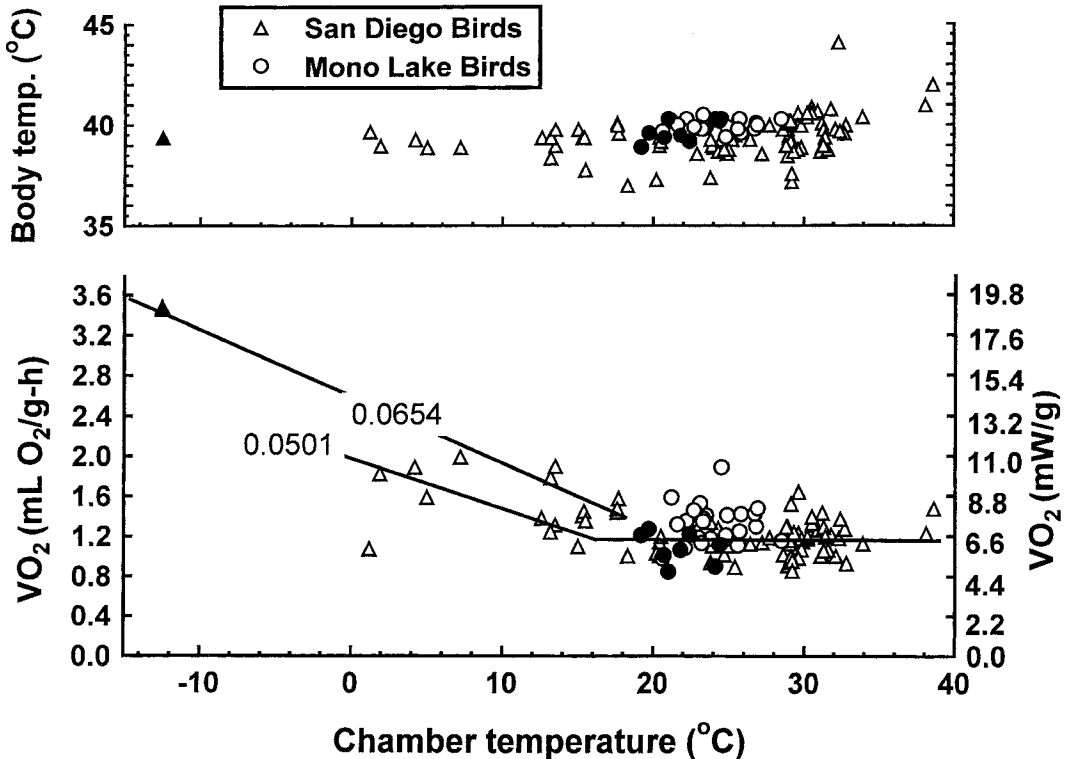


Figure 1. Thermoregulatory profile for 42 Eared Grebes in 121 experiments. The San Diego (N = 20) and Mono Lake (N = 22) measurements are noted separately; nighttime measures are filled symbols. All experiments below the thermal neutral zone (TNZ) were on San Diego birds. Thermal conductance values of 0.0654 and 0.0501 mL O₂/g·h·°C are shown next to the metabolic lines that they describe. A conversion to SI units is provided, using a conversion factor of 5.5 W/mL O₂, assuming RQ = 0.71 in postabsorptive birds.

highest value of 44.1°C was for a bird whose metabolic rate (1.186 mL O₂/g·h at air temperature = 32.3°C) did not suggest a problem arising from overheating.

DISCUSSION

Eared Grebes and many other nonpasserines fail to show the sizable circadian difference in metabolic rate first documented by Aschoff and Pohl (1970), and discussed by Ellis and Gabrielsen (2001). Although thermal conductance increased with molt, we could find no concomitant increase in BMR, unlike Lindström *et al.* (1993) and Klaassen (1995). This could be because most of our metabolic experiments (all for the San Diego birds) occurred in birds that were not molting remiges. Schieltz and Murphy (1997) reported that the White-crowned Sparrow (*Zonotrichia leucophrys*) did not show elevated metabolic rates if plumage replacement is low or temperatures are high. Perhaps because grebes are always in some stage of body molt (Storer and Jehl 1985), any additional cost associated with the main prebasal molt is too small to be detectable.

Because of its wide zone of thermoneutrality, the Eared Grebe is unlikely to be thermally stressed at autumn staging areas. Heat stress at Mono Lake is unlikely because air temperatures rarely reached 28°C and the birds can use the water, which never exceeds 22°C in the summer, as a heat sink. As nights become longer and colder in late autumn, the water cools appreciably, but by then grebes are obese and highly buoyant. They can also gain heat by sunbathing (Storer and Jehl 1985; Jehl 1988) or reduce heat loss by tucking their feet on their backs. Under extreme conditions, they can increase their heat production considerably as seen in the two individuals at -12.5°C that increased their oxygen consumption by 2.87 × BMR. That one grebe was able to maintain a low metabolic rate at 1.2°C (see Fig. 1) suggests that minimal thermal conductance might be even lower under some circumstances.

By winter, Eared Grebes generally have migrated south. However, if brine shrimp remain available, they will remain longer and a

few will attempt to overwinter; in one year, many grebes stayed into early February (Jehl 1988). Conditions in the staging areas in late autumn and winter must become even more demanding, as winds accompany colder temperatures in the air and water temperature continues to drop. We were unable to duplicate this combination of conditions in the laboratory. However, metabolic measurements of grebes sitting on water ranging from 5°C to 24°C showed no unequivocal influence of water temperature on metabolic rate (H. Ellis, unpubl.). We think this is probably the case with wild grebes as well, because they remain obese until shortly before migration and accordingly have buoyancy, which keeps them floating high. The fact that Eared Grebes will remain on their staging area into the winter, as long as prey are adequate, argues that cold climate does not dictate their distributions. The high cost of migration in this species (18-33 × BMR; Jehl *et al.* 2003) is more likely to discourage emigration, even in the face of harsh climate, until food requirements leave no other option.

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