



SLIDING VS STATIC COLD EXPOSURE AND THE MEASUREMENT OF SUMMIT METABOLISM IN BIRDS

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Abstract—1. Maximum cold-induced oxygen consumption (summit metabolism, $\dot{V}O_{2\text{sum}}$) of endothermic animals is elicited in helium-oxygen atmospheres either by exposing individual animals to a decreasing series of temperatures until oxygen consumption plateaus (Sliding Cold Exposure), or by exposing groups of animals to a single temperature within a range of temperatures (Static Cold Exposure), the lower portion of the range producing hypothermia in most, or all, individuals. It is not known whether these two methods produce similar values for $\dot{V}O_{2\text{sum}}$.

2. We measured $\dot{V}O_{2\text{sum}}$ by both sliding and static cold exposure methods in summer acclimatized Warbling Vireos (*Vireo gilvus*) and Gray Catbirds (*Dumetella carolinensis*).

3. Mean (\pm SD) values for $\dot{V}O_{2\text{sum}}$ generated by the two cold exposure methods were 4.39 ± 0.50 ml $O_2 \cdot \text{min}^{-1}$ ($n = 15$, Static) and 4.37 ± 0.61 ml $O_2 \cdot \text{min}^{-1}$ ($n = 6$, Sliding) for vireos, and 7.57 ± 0.84 ml $O_2 \cdot \text{min}^{-1}$ ($n = 13$, Static) and 7.17 ± 0.85 ml $O_2 \cdot \text{min}^{-1}$ ($n = 6$, Sliding) for catbirds. These values did not differ significantly for either species.

4. We conclude that both methods for measurement of $\dot{V}O_{2\text{sum}}$ produce similar results, and that both are appropriate measures of summit metabolism in birds. Copyright © 1996 Elsevier Science Ltd.

Key Word Index: Summit metabolism; cold exposure; Aves, Warbling Vireo; *Vireo gilvus*; Gray Catbird; *Dumetella carolinensis*; thermogenesis

INTRODUCTION

Maximum cold-induced oxygen consumption (=summit metabolism, or $\dot{V}O_{2\text{sum}}$) defines the capacity of endothermic animals for thermogenic heat production and is positively correlated with cold resistance (Marsh and Dawson, 1989). Historically, summit metabolism was difficult to measure because of the very low temperatures required to elicit maximal thermogenic output. However, with the advent of the helium-oxygen (helox) atmosphere technique for measuring $\dot{V}O_{2\text{sum}}$ (Rosenmann and Morrison, 1974), there has been a recent proliferation of studies involving measurement of summit metabolism in birds and mammals (Dawson and Smith, 1986; Koteja, 1986; Bozinovic and Rosenmann, 1989; Swanson, 1990, 1993, 1995; Bozinovic, 1992; Hinds and Rice-Warner, 1992; Sparti, 1992; Hinds *et al.*, 1993; Cooper and Swanson, 1994; Chappell and Bachman, 1995; Dutenhoffer and Swanson, 1996). In these studies, summit metabolism is routinely measured either by exposing individual animals to a decreasing series of temperatures in helox until oxygen consumption ($\dot{V}O_2$) plateaus or the animal

becomes hypothermic (Sliding Cold Exposure), or by exposing groups of animals to a single temperature within a range of helox temperatures (Static Cold Exposure). In the latter method, the lower temperatures within the experimental range produce hypothermia in a large proportion, if not all, individuals, and $\dot{V}O_2$ also plateaus over this range (see Dawson and Smith, 1986; Swanson, 1990 for examples). The advantage of the sliding method is that smaller sample sizes are required to determine $\dot{V}O_{2\text{sum}}$ than for the static method. The static cold exposure method, however, has the advantage of providing a measure of cold tolerance (in terms of the percentages of birds becoming hypothermic within a given time period at the different helox test temperatures) which is of interest in seasonal or geographic comparisons. Whether these two different methods of cold exposure generate similar values for summit metabolism is unknown, and consequently, comparisons of $\dot{V}O_{2\text{sum}}$ among avian species have not included all available values (Hinds *et al.*, 1993).

Comparison of summit metabolism values elicited by the two cold exposure methods on birds (or mammals) exposed to similar environmental or acclimation conditions should allow determination

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of whether these two methods produce similar results. If it can be demonstrated that both methods produce similar values for $\dot{V}O_{2\text{sum}}$ this will greatly facilitate comparison of summit metabolism among different bird species. It was our intent in this study to measure $\dot{V}O_{2\text{sum}}$ by both sliding and static helox cold exposure methods in two species of small to medium-sized passerine birds, the Warbling Vireo (*Vireo gilvus*) and the Gray Catbird (*Dumetella carolinensis*), acclimatized to summer (June–July) conditions in southeastern South Dakota to determine if the two cold exposure methods generate similar values for $\dot{V}O_{2\text{sum}}$ in these species.

METHODS AND MATERIALS

Birds

Vireos and catbirds were captured by mist-net before 1100 h (CST) near Vermillion, Clay County, South Dakota, USA (Scientific collecting permits: SD 95-11, USFWS PRT-758442) during summer 1995. Capture dates ranged from 12 June–24 July for vireos and 14 June–31 July for catbirds. All birds tested were adults (determined by plumage characteristics and skull ossification, Pyle *et al.*, 1987) and showed little evidence of molt. Birds were tested without regard to sex, because there was no apparent influence of sex on metabolic characteristics, but male:female sex ratios (determined by presence of brood patch or cloacal protuberance, Pyle *et al.*, 1987) for the different cold exposure treatments were 5:10 (Static) and 3:3 (Sliding) for vireos, and 8:5 (Static) and 3:3 (Sliding) for catbirds. Mass at capture was determined to the nearest 0.1 g on an Ohaus model LS-200 portable electronic balance. Following capture, birds were transported to the laboratory where metabolic tests were conducted on the day of capture between 0746 and 1419 h (CST). Prior to metabolic tests birds were given free access to food (*Tenebrio* larvae and mulberries, *Morus alba*) and water.

Cold exposure

Cold exposure tests were conducted in an atmosphere of 79% helium–21% oxygen (helox). Because helium has approximately 4-fold higher thermal conductivity than nitrogen, small endotherms lose heat to an helox atmosphere much more rapidly than to air, facilitating summit metabolism ($\dot{V}O_{2\text{sum}}$) at relatively moderate ambient temperatures (Rosenmann and Morrison, 1974). In this study, individual birds were subjected to helox cold exposure by one of two methods (static or sliding cold exposure). Both methods involved placing birds

into metabolic chambers fashioned from 1.9 L (vireos) or 3.8 L (catbirds) paint cans with the inner surface painted flat black to provide emissivities near 1.0. Helox was then passed through the chamber at metered rates and oxygen consumption ($\dot{V}O_2$) measured (see below). Chamber temperature was controlled by immersing the chamber into a bath of water/ethylene glycol capable of regulating bath temperature to $\pm 0.5^\circ\text{C}$. Chamber temperature was monitored continuously throughout cold exposure tests with a Cole-Parmer thermocouple thermometer (Model 8500-40, previously calibrated to a thermometer traceable to the U.S. Bureau of Standards) attached to a copper–constantan thermocouple inserted into the outlet port of the metabolic chamber. At the termination of all cold exposure tests, we measured body temperature (T_b) of the birds by inserting a 20-gauge copper–constantan thermocouple into the cloaca to a depth (approximately 1 cm) where further insertion did not alter the temperature reading. Prinzing *et al.* (1991) reported mean T_b for passerines as 41.6°C and 38.9°C , during the active and resting phases of the daily cycle, respectively. Mean nocturnal T_b at thermoneutrality for vireos was $37.8 \pm 1.2^\circ\text{C}$ ($n = 5$), and for catbirds was $39.9 \pm 0.5^\circ\text{C}$ ($n = 6$) (Swanson, unpubl. data). Because mean T_b is 2.7°C higher during the active phase than during the resting phase for passerines (Prinzing *et al.*, 1991) and $\dot{V}O_{2\text{sum}}$ was measured during the active phase, we considered birds with a $T_b < 37^\circ\text{C}$ as hypothermic.

For static cold exposure tests, individual birds were exposed to a single temperature in helox for 60 min or until they became hypothermic (indicated by a steady decline in $\dot{V}O_2$ over several minutes). Helox temperatures during static cold exposure tests were 10, 6, and 3°C for vireos, and 6, 2, and -1°C for catbirds. For sliding cold exposure tests, individual birds were exposed to a series of declining temperatures in helox, beginning at 8°C for vireos and 4°C for catbirds. The sliding cold exposure followed the same pattern in all birds: 25 min at the initial temperature, followed by 3°C decrements in bath temperature every 20 min thereafter. This pattern continued until $\dot{V}O_2$ leveled out at maximum rates (i.e. $\dot{V}O_2$ no longer increased with a further decrease in bath temperature). Sliding cold exposure tests were conducted for a maximum of 84 min. All birds exhibited T_b below 37°C at the termination of sliding cold exposure tests.

Oxygen consumption

Oxygen consumption was measured by open-circuit respirometry using an Ametek S-3A oxygen analyzer according to Swanson (1993). Flow rates of

dry, CO₂-free, helox from compressed gas cylinders were metered through metabolic chambers at 1015–1025 ml·min⁻¹ by a Cole-Parmer precision rotameter (Model FM082-03ST), previously calibrated to +1% accuracy (Swanson, 1990), located upstream from the metabolic chamber. These flow rates kept the fractional concentration of oxygen in excurrent gas above 20.15%. Prior to immersion of the metabolic chamber into the bath to initiate cold exposure tests, the chamber was flushed with helox at these flow rates for at least 5 min. Fractional concentration of oxygen in excurrent air was measured every 60 sec over the cold exposure tests. Oxygen consumption was calculated as instantaneous $\dot{V}O_2$ according to Bartholomew *et al.* (1981), following the procedure of Dawson and Smith (1986). Effective volumes of the metabolic chambers and associated tubing in the absence of a bird (also calculated according to Bartholomew *et al.*, 1981) were 2063 ml for the 1.9 L chamber and 3774 ml for the 3.8 L chamber. Oxygen consumption was averaged over 10-min intervals (1–10, 2–11, etc.) throughout the cold exposure tests, and the highest 10-min mean over the test period was considered $\dot{V}O_{2sum}$. The first 10 min were excluded from calculations of $\dot{V}O_2$ to allow excurrent oxygen concentration readings to stabilize. All values for $\dot{V}O_2$ were corrected to STP.

Statistics

Data are reported as means \pm SD. Oxygen consumption is reported as both total (per-bird) and mass-specific $\dot{V}O_2$. Comparison of $\dot{V}O_{2sum}$ and body mass at the different helox temperatures used for static cold exposure tests was by ANOVA, or

Kruskal-Wallis test if variances differed significantly (F-test). Comparison of $\dot{V}O_{2sum}$ and body mass between static and sliding cold exposure treatments was by Student's *t*-test because variances were not significantly different (F-test). Statistical significance was accepted at $P \leq 0.05$.

RESULTS

Body mass did not differ significantly among different static cold exposure temperatures for either species, so values were pooled to provide a single mean mass for static cold exposure for each species. These values were 13.4 \pm 0.7 g for vireos (n = 15) and 33.1 \pm 1.6 g for catbirds (n = 13). Mean masses for sliding cold exposure birds were 13.4 \pm 0.4 g for vireos (n = 6) and 35.1 \pm 2.4 g for catbirds (n = 6). Mean mass did not differ significantly between cold exposure treatment for vireos, but catbirds subjected to sliding cold exposure were significantly ($P < 0.05$) heavier than those subjected to static cold exposure. Thus, comparisons of $\dot{V}O_{2sum}$ were carried out on both total (per-bird) and mass-specific bases.

Neither vireos nor catbirds showed significant differences in $\dot{V}O_2$ among static cold exposure temperatures (Fig. 1), so values were pooled for $\dot{V}O_{2sum}$. Pooled static $\dot{V}O_{2sum}$ was 4.39 \pm 0.50 ml O₂·min⁻¹ (19.67 \pm 2.21 ml O₂·g⁻¹·h⁻¹, n = 15) for vireos and 7.57 \pm 0.84 ml O₂·min⁻¹ (13.70 \pm 1.35 ml O₂·g⁻¹·h⁻¹, n = 13) for catbirds. Mean $\dot{V}O_{2sum}$ elicited by sliding cold exposure was 4.37 \pm 0.61 ml O₂·min⁻¹ (19.67 \pm 3.11 ml O₂·g⁻¹·h⁻¹, n = 6) for vireos and 7.17 \pm 0.85 ml O₂·min⁻¹ (12.28 \pm 1.61 ml O₂·g⁻¹·h⁻¹, n = 6) for catbirds. Mean values for $\dot{V}O_{2sum}$ elicited by static and sliding cold exposure methods did not

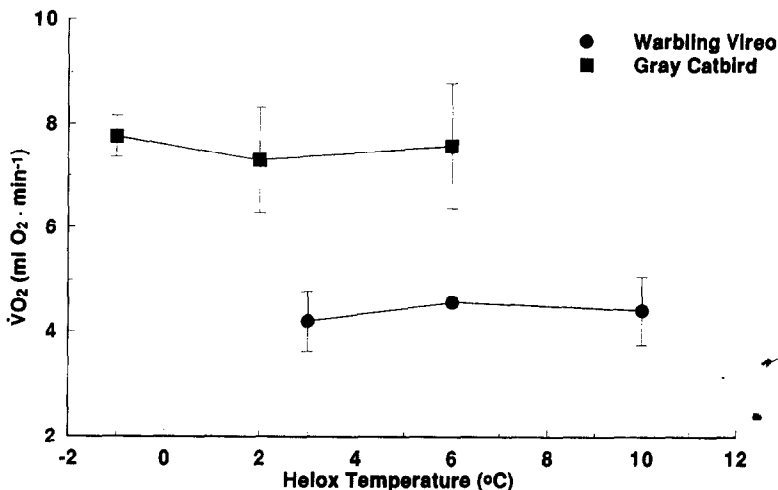


Fig. 1. Oxygen consumption at different temperatures in helox for summer acclimatized Warbling Vireos and Gray Catbirds. Oxygen consumption did not differ significantly among the different helox temperatures for either species.

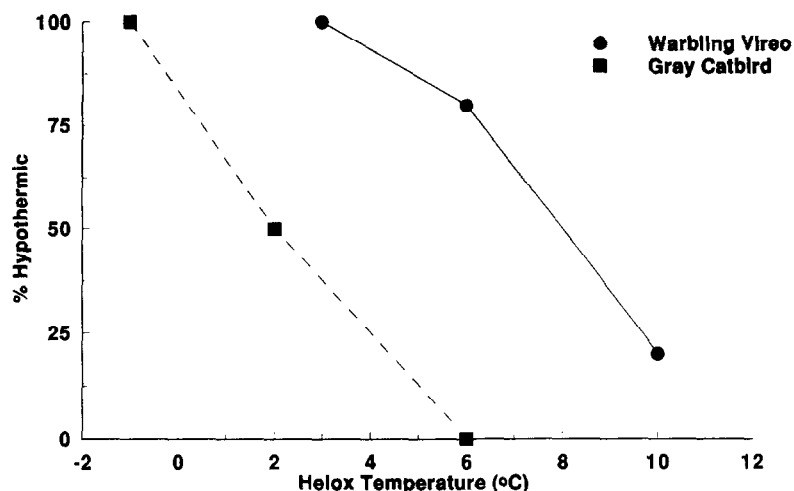


Fig. 2. Cold tolerance in summer acclimatized Warbling Vireos and Gray Catbirds over 1 h static helox cold exposure tests. No catbirds became hypothermic at 6°C. Five vireos were tested at each helox temperature, and sample sizes for catbirds were $n = 4$ at 2 and 6°C and $n = 5$ at -1°C.

differ significantly for either species, although mass-specific $\dot{V}O_{2sum}$ in catbirds approached significance ($P = 0.06$).

For both vireos and catbirds, an increasing proportion of birds became hypothermic at colder helox temperatures during static cold exposure (Fig. 2). Catbirds tolerated colder temperatures in helox than vireos. The better cold tolerance of catbirds was undoubtedly at least partially due to their approximately 25-fold larger body mass and the associated allometric decrement in relative surface area and increment in insulation (Aschoff, 1981).

DISCUSSION

Several previous studies investigating seasonal acclimatization in birds have documented seasonal changes in cold tolerance and accompanying seasonal changes in $\dot{V}O_{2sum}$ measured by static helox cold exposure (Dawson and Smith, 1986; Swanson, 1990, 1995; Cooper and Swanson, 1994; Liknes, 1994). Other studies have generated $\dot{V}O_{2sum}$ by sliding helox cold exposure for various experimental reasons (Koteja, 1986; Hinds *et al.*, 1993; Dutenhoffer and Swanson, 1996). Hinds *et al.* (1993) generated allometric equations relating $\dot{V}O_{2sum}$ to body mass in different groups of endotherms, including birds, but excluded all data measured by static helox cold exposure or cold exposure in air from calculation of these equations, presumably due to potential discrepancies in $\dot{V}O_{2sum}$ measured by different techniques and/or phylogenetic effects. Our data indicate that sliding and static helox cold exposure do not produce significantly different levels of $\dot{V}O_{2sum}$ in

vireos or catbirds. This suggests that both cold exposure methods provide appropriate measures of $\dot{V}O_{2sum}$, and that $\dot{V}O_{2sum}$ values elicited by both methods can be used in comparative analyses.

Previous studies using sliding helox cold exposure to elicit $\dot{V}O_{2sum}$ in birds (Koteja, 1986; Hinds *et al.*, 1993) have implied that hypothermia is necessary as an experimental endpoint to ensure that summit metabolism has been attained. Hinds *et al.* (1993) also suggest that $\dot{V}O_{2sum}$ generally occurs just prior to the decline in $\dot{V}O_2$ indicative of hypothermia. However, static cold exposure studies indicate a plateau of $\dot{V}O_2$ at summit metabolism levels over a relatively small range of helox temperatures, the lower temperatures within this range producing hypothermia in most or all individuals, the upper temperatures producing hypothermia in a smaller fraction of individuals (Rosenmann and Morrison, 1974; Dawson and Smith, 1986; Swanson, 1990, 1993, 1995; Cooper and Swanson, 1994). These latter studies suggest that hypothermia in all individuals is not required as an endpoint to validate $\dot{V}O_{2sum}$ measurement by static cold exposure in small birds, as long as temperatures are within the range where $\dot{V}O_2$ plateaus. In fact, temperatures producing rapid hypothermia failed to elicit maximal thermogenic output (Dawson and Smith, 1986; Koteja, 1986; Swanson, 1990). Our experience indicates that a good general rule for static helox cold exposure is that temperatures producing hypothermia within 1 h in 40 to 60% of individuals are included within the $\dot{V}O_{2sum}$ plateau and, therefore, provide effective measures of mean $\dot{V}O_{2sum}$ for the population under study (Swanson, 1990, 1993, 1995; Cooper and Swanson, 1994; Liknes, 1994). However, in studies addressing

Table 1. Comparison of time to the beginning of the highest 10-min mean $\dot{V}O_2$ over the test period (Time_{sum}) and time to termination of the cold stress test and removal from the metabolic chamber ($\text{Time}_{\text{removal}}$). The duration of cold exposure required to elicit summit metabolism generally was substantially shorter than the period required to induce a decline in metabolism indicative of hypothermia.

Species	<i>n</i>	Cold exposure temperature (°C)	Time_{sum} (min)	$\text{Time}_{\text{removal}}$ (min)*
Vireo	5	10	32 ± 10	60
	5	6	26 ± 15	56 ± 8
	5	3	13 ± 4	34 ± 8
	6	Sliding (≤8)	20 ± 11	47 ± 14
Catbird	4	6	25 ± 12	60
	4	2	19 ± 6	52 ± 9
	5	-1	17 ± 4	50 ± 6
	6	Sliding (≤4)	22 ± 9	62 ± 13

* All birds at the highest static helox temperatures maintained oxygen consumption over the entire 60 min test period, and all birds except one vireo ($T_b = 36.7^\circ\text{C}$) were normothermic ($T_b > 37^\circ\text{C}$) on removal from the chamber at these temperatures. At 6°C , 4 of 5 vireos lasted the entire 60 min, but only 1 remained normothermic (Fig. 2). At 2°C , 2 catbirds lasted the entire 60 min and both were normothermic, while at -1°C , 1 catbird lasted 60 min but was hypothermic ($T_b = 36.8^\circ\text{C}$) on removal from the chamber.

individual variation in thermogenic capacity, sliding cold exposure is the more appropriate measure of $\dot{V}O_{2\text{sum}}$, because it accounts for individual variation.

Sliding cold exposure in this study produced hypothermia in all individuals tested, and colder static cold exposure temperatures also produced hypothermia in a majority of individuals. However, $\dot{V}O_{2\text{sum}}$ did not occur immediately before the decline in $\dot{V}O_2$ indicating hypothermia in either static or sliding cold exposure tests, but occurred much earlier in the test period (Table 1). Instead of a rapid decline in $\dot{V}O_2$ immediately following $\dot{V}O_{2\text{sum}}$, the entrance into hypothermia was a more gradual process occurring over longer time periods. Dutenhoffer and Swanson (1996) used sliding helox cold exposure to measure $\dot{V}O_{2\text{sum}}$ in a number of passerine birds and also found that $\dot{V}O_{2\text{sum}}$ occurred far earlier in cold exposure tests than did the decline in $\dot{V}O_2$ indicative of hypothermia. Thus, it appears that hypothermia is not a necessary endpoint to validate $\dot{V}O_{2\text{sum}}$ for sliding cold exposure either. We suggest that an appropriate experimental endpoint for sliding cold exposure occurs when $\dot{V}O_2$ no longer increases with further decreases in helox temperature. Our experience indicates that if this condition is met it can be safely assumed that $\dot{V}O_{2\text{sum}}$ has been attained.

Because $\dot{V}O_{2\text{sum}}$ did not differ significantly between static and sliding cold exposure in this study, we pooled measurements to yield $\dot{V}O_{2\text{sum}}$ values of $4.38 \pm 0.52 \text{ ml O}_2 \cdot \text{min}^{-1}$ ($19.7 \pm 2.4 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, $n = 21$) for vireos and $7.44 \pm 0.84 \text{ ml O}_2 \cdot \text{min}^{-1}$ ($13.25 \pm 1.55 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, $n = 19$) for catbirds. These values were not significantly different (Student's *t*-test, $P > 0.05$) on either per-bird or mass-specific bases from previously reported $\dot{V}O_{2\text{sum}}$ for summer acclimatized Warbling Vireos (Swanson,

1995) or Gray Catbirds (Dutenhoffer and Swanson, 1996).

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