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Woodpecker cavity aeration: a predictive model

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Abstract

We studied characteristics of the Syrian woodpecker (*Dendrocopos syriacus*) cavities in the field and a laboratory model, and rates of gas exchange in the laboratory. Night temperature of occupied cavities is 4.3 °C higher than empty ones, representing energy savings of ~24%. Oxygen conductance ($G_{\mathrm{NO_2}}$) of an empty cavity is 7.1 ml$_{[\mathrm{STPD}]}$ (Torr h)$^{-1}$, and is affected by winds at velocities up to 0.8 m/s. Day and night body temperatures were 42.0 and 40.1 °C, respectively. Steady-state O_2 consumption rates ($\dot{M}_{\mathrm{O_2}}$) were 3.49 ± 0.49 and 2.53 ± 0.26 ml$_{[\mathrm{STPD}]}$ (g h)$^{-1}$ during day and night respectively – higher than predicted by allometry. A mathematical model describing $P_{\mathrm{O_2}}$ in a cavity, taking into consideration $\dot{M}_{\mathrm{O_2}}$, $G_{\mathrm{NO_2}}$, heat convection and wind speed, from the moment birds inhabit it, was developed. It shows that on the average, one woodpecker staying in its cavity at night does not encounter hypoxic conditions. However, in nest cavities with below the average $G_{\mathrm{NO_2}}$, with more inhabitants (e.g. during the breeding season), hypoxia may become a problem.

Keywords: Birds, Syrian woodpecker (*Dendrocopos syriacus*); Environment, confinement; Gas exchange, Model, Nest aeration; Cavity-dewelling

1. Introduction

Many animals, such as cavity-nesting birds and fossorial mammals, spend at least some of their time in spaces partially closed off from ambient air. These shelters help reduce activity as they protect from enemies and extreme climatic conditions. In addition, during the breeding season, they provide shelter for the young. For birds, these spaces may have additional safety benefits when incubating eggs. However, for animals that live in self-constructed closed spaces, the cost of construction has to be considered (Andersen and MacMahon, 1981; Vleck, 1981). Furthermore, within these closed spaces, hypoxia and hypercapnia may develop as the organisms consume O_2 and produce CO_2. If these respiratory gases are not fully restored in animal burrows, cavities or holes, O_2 and CO_2 pressures become lower and higher respectively, relative to free air values. The animal may then need to adapt to live in such conditions (Withers, 1977; White et al., 1978; Wilson and Kilgore, 1978; Furilla, 1979; Wickler and Marsh, 1981;

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Birchard et al., 1984; Ar, 1987, 1992; Howe et al., 1987; Howe and Kilgore, 1987; Ar and Piontkewitz, 1992; Mersten-Katz, 1997a). White et al. (1978) have suggested that in poorly ventilated burrows and cavities, NH_3 may build up as a result of the presence of feces, droppings, decomposition of food remains and high humidity. The burrow atmosphere of bee-eaters may reach up to 0.5 Torr ammonia, which could be harmful to its inhabitants.

Adaptations to life in confined spaces may be arranged in three main groups: conforming, avoiding behaviorally and/or coping physiologically with the respiratory stress (Prosser, 1973; Ar, 1992). Most mammals that live in confined spaces dig burrows in soil. Depending on body mass, type of soil and their activities, these fossorial mammals may encounter and cope with various degrees of hypoxia and hypercapnia (Hall, 1966; McNab, 1966; Faleschini and Whitten, 1975; Morrison and Rosenmann, 1975; Arieli et al., 1977; Vleck, 1979; Jelkmann et al., 1981; Maclean, 1981a, b; Hayssen and Lacy, 1985; Contreras, 1986). Coping with a hypoxic-hypercapnic atmosphere may require several adaptations along the pathway of O_2 and CO_2 from the ambient atmosphere to the mitochondria and vice versa. These adaptations may include reduced energy metabolism, or dead space, increased ventilation, lung diffusion capacity, cardiac output, Bohr effect, blood buffering, O_2 capacities, hemoglobin affinity, capillary density, tissue myoglobin, and changes of chemoreflex sensitivities. So far, only some of these have been investigated in animals living in confined spaces.

Oxygen consumption of animals living in confined spaces tends to be lower than predicted by allometry, thus reducing the need for oxygen and increasing the metabolic scope. This is true mainly for mammals (reviewed by Ar, 1987; Withers et al., 2000), while in birds the situation is not clear.

The response of the ventilatory system to a confined atmosphere is attenuated. The threshold for increased ventilation is shifted to relatively high ambient CO_2 pressures in fossorial mammals (Parer and Metcalfe, 1967; Darden, 1972; Maclean, 1978; Arieli and Ar, 1979). Again, in birds the situation is less clear. Boggs and Kilgore (1983) showed a high threshold of ventilatory response P_{ICO_2} and a reduced ventilatory response to hypoxia in the burrowing owl, as compared to a reduced ventilatory response to CO_2 in the non-burrow dwelling bobwhite. Furilla (1979) found a similar effect in bank swallows.

Cardiac output of fossorial mammals is significantly lower than predicted and this is also true for their heart rate. The low heart rate of the mole rat has been attributed to a high parasympathetic vagal tone (Storier et al., 1981). These unexpected results may be explained by a higher cardiac output scope that can be achieved during digging activities. This idea is supported by observations showing that oxygen consumption during such activity reaches values up to seven times higher the basal metabolic rate (reviewed by Ar, 1987; Marhold and Nagel, 1995; Seymour et al., 1998; Ebensperger and Bozinovic, 2000). To the best of our knowledge, there are no comparable studies of cardiovascular adaptations in birds that live in confined spaces.

Blood adjustments found in fossorial mammals include a relatively high O_2 affinity which results in part from low 2,3-DPG to Hb ratio. However, O_2 capacity and its constituents do not show a specific trend. Despite the high blood P_{CO_2}, blood pH in fossorial mammals is in the normal range, indicating a high buffer capacity and high bicarbonate level in their blood (reviewed by Ar, 1987). High bicarbonate may explain in part the shift in CO_2-threshold for increased ventilation. Of the two P_{50} values known for birds that live in confined spaces, one was in the normal range of oxygen affinities for birds, while the other was significantly higher. Here too, O_2 capacities (Hb concentrations) are not significantly higher than predicted, and burrow dwelling birds have normal Bohr factors (Boggs et al., 1984). Nevertheless, polycythemia was found in the mole rat (Ar et al., 1977); however, since the mole rat shows an increase in erythrocyte volume (Arieli and Ar, 1979) no general trend can be assigned to fossorial mammals. Lutz and Storey (1997) noted that, even under normal atmospheric conditions (in which many experiments are performed), some burrowing mammals maintain low Pa_{O_2} and high Pa_{CO_2} values, showing a shift in ventilatory and blood-gas set points.

At the tissue level of fossorial mammals, Arieli and Ar (1981) found high heart and muscle capillary density, and elevated muscle myoglobin concentrations were found by Ar et al. (1977) and Lechner (1976). Comparative data do not exist for birds. Perhaps one of the most important features of animals living in confined spaces is their general ability to tolerate severe hypoxic-hypercapnia (Arieli and Kerem, 1984).

In this sense, they may resemble diving animals and embryos.

In contrast to the brush turkey and the mallee fowl, which incubate their eggs inside mounds of decomposing organic materials and, as a result, the atmosphere around the eggs is low for O_2 and high for CO_2 (Seymour and Ackerman, 1980), some fossorial mammals and birds which inhabit burrows may benefit from gas exchange of their burrows by diffusion through the soil walls (Boggs et al., 1984; Tenney and Boggs, 1986; Ar and Piontkewitz, 1992). Even though European bee-eaters ventilate their soil cavities, O_2 levels in them may stay low and CO_2 levels remain high (Ar and Piontkewitz, 1992). However, most birds inhabiting tree cavities must rely on gas exchange through a single opening. Since diffusive rates of respiratory gases through wood are negligible (Banks, 1968), relatively low O_2 levels and high CO_2 levels might be encountered by birds staying within tree cavities. Yom-Tov and Ar (1993) suggested that the relatively short incubation period typical to woodpeckers is an adaptation to the apparently poor gas exchange in the nest cavity with a parent incubating the eggs. Indeed, Mersten-Katz (1997a) measured O_2 concentrations ranging from 17.6 to 20.6% and CO_2 concentrations of 0 to 2.2% at the bottom of natural nest cavities of the Syrian woodpecker.

The Syrian woodpecker (*Dendrocopos syriacus*) is a Mediterranean avian species, which constructs and inhabits tree cavities throughout the year at nights, and uses them as nests during the breeding season. In the following discussion, 'cavity' will be used for a roosting home of a single bird, and 'nest cavity' for a nesting place from incubation until fledging. The woodpecker resides at the bottom of its cavity, which is open to free air only through a narrow entrance. Therefore, it can be hypothesized that the atmosphere within the tree cavity of the Syrian woodpecker is hypoxic and hypercapnic in comparison to atmospheric air. This must be true particularly during the breeding season when the nest cavity is occupied by a parent and a few nestlings, all of whom consume O_2 and produce CO_2.

The aim of this work was to model the gas composition in a woodpecker cavity as a function of its average dimensions, the gas exchange and heat conduction of an inhabiting bird at various cavity temperatures, and the influence of wind velocity on cavity gas composition. For this, we measured natural cavities in the field and accordingly designed an artificial cavity in the laboratory, of similar dimensions. In this artificial cavity we carried out measurements of its O_2 conductance (G_{sO_2}), and investigated how wind speeds and heat convection due to inhabitant heat production affect O_2 conductance. In addition, we measured the rate of O_2 uptake and CO_2 output of the woodpecker, and incorporated these values into the model.

2. Methods

2.1. Study sites and climate

The Syrian woodpecker lives in Israel in a temperate Mediterranean climate. Syrian woodpecker cavities were observed within a radius of about 50 km around Tel-Aviv, Israel. Mean maximal daily temperatures range between 17 °C in January to 31 °C in August, and mean minimal temperatures are from 7 to 22 °C, respectively. Average precipitation is 500–600 mm per annum and 85% of this precipitation falls within 50–60 days in the winter time (courtesy of Israel Meteorological Service).

2.2. Cavity measurements

Natural woodpecker cavities were measured in the field: the tree species was identified and height of the cavity above the ground was estimated. Horizontal and vertical entrance diameters, entrance length (frontal cavity wall) and cavity diameter were measured using a ruler, a caliber, and a home-made periscope which had a small flashlight at its end. A thread with a weight tied to its end was inserted down to bottom of the cavity, in order to measure depth. These measurements were accurate to ±0.2 cm. Volume of the cavity below the entrance was measured using a large polyethylene bag, which was inserted into the cavity and filled with water through an elastic tube up to the rim of the entrance opening. Water was then drained from the plastic bag into a graduated cylinder and measured (±10 ml).

2.3. An artificial cavity in the laboratory

Similar to the dimensions of the natural woodpecker tree cavities (see Section 3, Table 1 and Fig. 1A), an artificial cavity was designed and built in the laboratory (Fig. 1B). The artificial cavity had a volume of 2.71

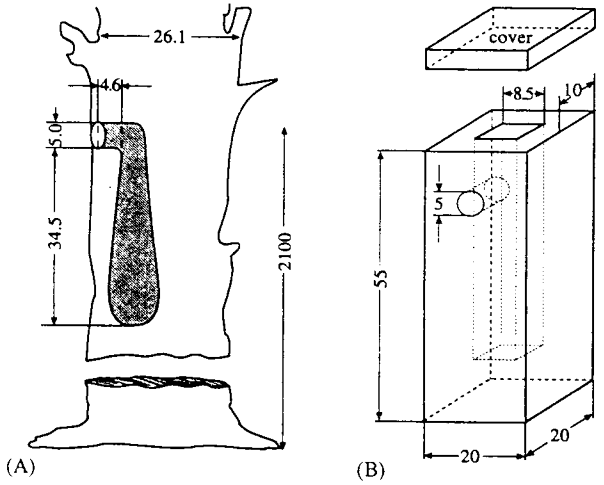

Fig. 1. (A) A diagram of an average natural woodpecker cavity. (B) A diagram of the artificial nest cavity used in the laboratory experiments (values are dimensions in cm).

below the bottom of the entrance. Its box was made from pinewood, and the inside surface was pitted with a pointed hammer to produce a rough surface upon which the woodpecker could climb.

2.4. *Bird handling in captivity*

Eleven nestlings were collected in the wild from natural Syrian woodpecker nest cavities according to permits received from the Nature Reserves Authority and transferred to the Canadian Center for Ecological Zoology of the Department of Zoology at Tel-Aviv University. There, the young birds were hand-reared until they were mature enough to feed on their own. Birds were fed daily with 'omelet' strips made from eggs, fly maggots, meal worms and seed mixture, and were given water and food ad libitum. They were then transferred into large outdoor cages (5 m (W) × 5 m (L) × 4 m (H)), equipped with posts, stands, and artificial cavities. After a period of adjustment, conditions in captivity were good enough to allow breeding. Five adults were used for collecting experimental data in the laboratory.

2.5. *Diffusive O_2 conductance in the artificial cavity*

Before use, the artificial cavity box was checked for possible gas leaks. All leaks were sealed, except for the opening. This is in contrast to the northern flicker natural cavities used by Howe and Kilgore (1987), where significant gas diffusion occurred through the walls. The measurements were made using the principle and equations of Wangensteen et al. (1970/1971).

To measure diffusive cavity O_2 conductance (G_{NO_2D}; ml (Torr h)$^{-1}$) the cavity box was positioned vertically, filled with nitrogen and then left to refill with room air (Ar and Piontkewitz, 1992). Care was taken to maintain still air around the site of the experimental set-up. Changes in O_2 concentrations in the cavity with time were measured and recorded graphically using a Beckman oxygen electrode connected to a Beckman Fieldlab O_2 analyzer and a Perkin-Elmer 165 recorder. The electrode was inserted through the entrance and situated vertically face down just above the bottom of the cavity box. Water drops were added to create a humid atmosphere inside the cavity box, so that the electrode would not dry out during the experiments.

O_2 wash-in process was calculated according to the following mathematical model that assumed: (1) total gas pressure is equal within the cavity and in the free air; (2) diffusion rate of N_2 out of the cavity equals diffusion rate of O_2 into the cavity; (3) gas diffusion behaves as an ideal two-compartment system, where the two compartments are the artificial cavity and the surrounding atmosphere; the latter is infinitely large and of constant composition, and the enclosed cavity compartment is well mixed. Eq. (1) describes the change in O_2 pressure at the bottom of the cavity box ($P_{NO_2(t)}$; Torr) with time (t; h):

$$P_{NO_2(t)} = P_{AO_2}(1 - e^{-G_{NO_2D}t}), \qquad (1)$$

where P_{AO_2} (Torr) is O_2 pressure in the atmosphere around the cavity and is known. Since all other equation constants and parameters are measured, G_{NO_2D} is calculable (Ar and Piontkewitz, 1992).

2.6. *Effects of wind and heat convection on overall cavity O_2 conductance (G_{NO_2})*

The effects of wind on O_2 refill into the artificial cavity (and thus on G_{NO_2}) were determined using an electric fan and a calibrated digital Testo 490 Instant Action Anemometer (accuracy = 0.05 m s^{-1}). Wind at velocities of about 0, 0.1, 0.2, 0.4, 0.8, and 1.6 m s^{-1} was directed frontal to the cavity opening and sideward at a 90° horizontal angle to the cavity opening. The anemometer probe tip was placed at the center of the external opening of the entrance.

The effect of heat convection on G_{NO_2} was determined using the same method as above. In this case, a temperature controlled home-made electrical heating element was used to create the heat production rate comparable to that of a woodpecker at rest occupying the cavity. The heating element was placed within an insulated plastic container (4 cm in diameter, 10 cm of height) filled with 73 g of water (an average woodpecker mass in nature; Barnea, 1982). The container was wrapped with styrofoam and a wool sock for insulation. Final dimensions were 11.2 cm height and 5.5 cm in diameter. The heating element was kept heated at a core temperature of 40.1 ± 0.1 °C (average of day and night body temperatures, see Section 3) for at least 1 h until steady-state heat flux and heat convection was achieved.

The G_{NO_2} value determined in this experiment is assumed to be an additive combination of both G_{NO_2D} and convective O_2 conductance due to heat produced by the cavity inhabitant (G_{NO_2H}). Using this assumption, it is possible to quantitatively determine the G_{NO_2H} by subtracting G_{NO_2D} from $G_{NO_2(D+H)}$.

G_{NO_2} of a given wind speed (G_{NO_2W}) near the cavity opening can be calculated using a similar assumption:

$$G_{NO_2(W+D+H)} = G_{NO_2(W+D)} - G_{NO_2H}, \qquad (2)$$

where $G_{NO_2(W+D)}$ is the conductance at a given wind speed, which itself is a combination of G_{NO_2D} and G_{NO_2W}, and $G_{NO_2(W+D+H)}$ is the combined G_{NO_2} of wind effect, diffusion, and heat conductance. Note that G_{NO_2H} and G_{NO_2W} are the same for all gases while G_{NO_2D} is particular for O_2.

2.7. Laboratory measurements of mass-specific oxygen consumption ($\dot{M}_{O_2}$) and CO_2 production ($\dot{M}_{CO_2}$) rates

Two birds at a time were kept individually in cages (70 cm (*W*) × 70 cm (*L*) × 55 cm (*H*) each) in a temperature and light controlled chamber, and fed as described above. To resemble breeding season days (spring), the light regime was 14*L*:10*D*. While field temperatures change during the woodpeckers' breeding season from a minimum of 11–15 °C during nights and maximum of 25–28 °C during days (courtesy of Israel Meteorological Service), actual temperatures inside the cages were 10.7–13.7 °C at night and 24.5–25.8 °C during the day.

Since the purpose of $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ experiments was to determine the actual metabolic needs of the woodpecker while in its cavity in nature, neither night nor day experiments were done on post-absorptive animals.

The experimental set-up consisted of a 2 l metabolic chamber through which room air was drawn by means of an air pump. The flow (600–660 ml min^{-1}) was directed in series through a Drierite column, to a calibrated Matheson Flow Meter, model 700-BBV (Montgomeryville, PA, USA; precision = ±3 ml min^{-1}), and through a calibrated Servomex O_2 analyzer 570A (East Sussex, England; accuracy = ±0.05%) and a calibrated Servomex CO_2 analyzer, series 1400 (East Sussex, England; accuracy = ±0.05%). The outputs were simultaneously recorded onto a Zipp & Zonen Recorder (Delft, The Netherlands).

Temperature inside the metabolic chamber (T_A) was controlled using a copper coil by a Julabo temperature controlled water-bath model EO7 EC/F10 (JD Instruments Inc., Houston, TX). A Bailey thermocouple reader model Bat 8 (Delray Beach, FL, USA) was used in conjunction with two thermocouples (precision of ±0.05 °C) to measure T_A and body temperature (T_b). Body mass was measured with a Mettler Toledo digital scale model BB120 (Columbus, OH, USA; accuracy of ±0.5 g) after every experiment. Barometric pressure was noted for STPD calculations.

For measurements, a bird was placed into a dark metabolic chamber. A calibrated thermocouple, placed within the metabolic chamber, continuously measured its temperature. Preliminary experiments showed that a bird had to be kept in the metabolic chamber for 75 min for stabilization of the chamber temperature and the metabolism of the bird, before measurements were made. Thereafter, mean minimal reduction of percent O_2 recording values, indicating rest periods, were averaged for $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ calculations. $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ calculations were made using data from the O_2 and CO_2 analyzers and the flow which was adjusted to STPD conditions (after Vleck, 1987), and all calculated gas values were expressed at STPD conditions.

The respiratory quotient (RQ) was calculated from $RQ = \dot{M}_{CO_2} \cdot \dot{M}_{O_2}^{-1}$. At the end of each experiment, T_b was measured by inserting a calibrated and lubricated thermocouple approximately 1.5 cm into the cloaca of the bird. In order to keep the bird calm and to get an immediate reading, the bird was held inside a cloth bag. The entire procedure lasted approximately 1 min.

Heat conductance (C_b) of the woodpecker was calculated as the slope of the curve of woodpecker $\dot{M}_{O_2}$ as a function of T_A, below the thermoneutral zone. This curve was fitted to intercept the x-axis at $T_A = T_b$, and go to a point that describes the average values of all temperatures of measurements below $T_A = 20\,°C$, and the average of the corresponding $\dot{M}_{O_2}$ values. The $\dot{M}_{O_2}$ values included in the average calculations were only those that were at least one S.D. higher than the average values obtained between $T_A = 20$ and 35 °C (approximately indicating the TNZ). Day and night C_b were calculated separately.

Upper critical temperatures (UCT, °C) were defined by the points at which T_b and $\dot{M}_{O_2}$ rose above normal. Lower critical temperatures (LCT, °C) were defined at the intercept between the TNZ horizontal line and the C_b slope on the $\dot{M}_{O_2}$ versus T_A regression line.

2.8. *Statistical analyses*

In order to facilitate comparisons with the literature cited, the pressure data is given in torrs where the conversion factor to SI units is: 1 Torr = 0.133322 kPa.

The choice of statistical significance tests is indicated in the appropriate places in Section 3. Results are expressed as means ± standard deviation.

3. Results

3.1. *Natural cavities*

Data for 19 natural cavities are summarized in Table 1. Margos (*Melia azedarach*) and Carobs (*Ceratonia siliqua*) were popular tree species, possibly because of their soft timber (Y. Reves, personal communication). Seven and four cavities were found in each, respectively. A slight preferred orientation towards east–south–east (sunrise direction) was found for the direction of cavity opening (Fig. 2). The cavity opening was usually facing an open and lighted area. Year round, woodpeckers entered their cavities 31 ± 10 min ($n = 7$) before sunset and left the cavity at about half an hour after sunrise. Height of the cavity opening from the ground was between 1 and 4 m. A schematic representation of an averaged natural cavity is given in Fig. 1A. The mean thickness of the frontal cavity wall was 4.6 ± 2.1 cm, its mean depth was 34.5 ± 7.5 cm and the volume below the entrance was 2.2 ± 0.6 l. The vertical and horizontal diameters of the round cavity opening were, in general, very uniform (5.0 ± 0.5 cm × 4.8 ± 0.5 cm, respectively).

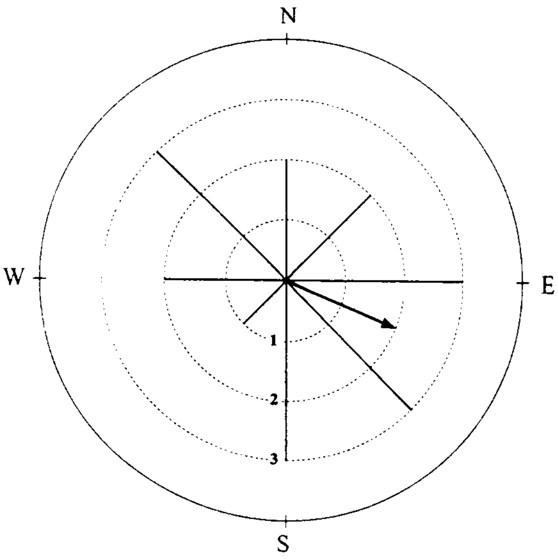

Fig. 2. Distribution of the direction of cavities' openings. The arrow represents the mean vector. Length of each radius represents the number of cavities facing a given direction.

Night temperatures of two unoccupied cavities were measured continuously, twice each, and found to be identical to ambient temperatures. Night temperatures of 11 occupied cavities were measured and compared to ambient temperatures. The results, summarized in Table 2, show that temperatures in occupied cavities were always higher than ambient ones (average difference was 4.3 ± 1.9 °C, with no seasonal variation).

3.2. *Cavity oxygen conductance (G_{NO_2}) in the artificial cavity in the laboratory*

Cavity diffusive O_2conductance. G_{NO_2D} of the average artificial woodpecker cavity with an empty cavity in still air was found to be 7.1 ± 1.0 ml (Torr h)$^{-1}$ ($n = 8$).

The effect of wind on G_{NO_2} in an average artificial woodpecker cavity is summarized in Table 3, which

Table 1
Dimensional characteristics of natural cavities of the Syrian woodpecker

Nest no.	Tree species[a]	Nest entrance orientation	Height from ground (m)	Entrance diameter (cm)		Frontal cavity wall thickness (cm)	Cavity diameter at entrance (cm)	Depth of cavity below entrance (cm)	Volume below entrance (l)	Tree circumference at nest entrance (cm)
				Vertical	Horizontal					
1	M.a.	E	2.2	5	4.2	6	8	40	3	96
2	M.a.	SE	1.5	5.5	4.5	8.5	7	39	1.6	75
3	M.a.	NW	1.9	5.5	4.1	3	8	39	1.5	53
4	M.a.	S	1.1	5.5	5.0	8	10	41	3.1	79
5	M.a.	NE	3.1	4.5	4.5		10	26	1.7	76
6	M.a.	SE	1.6	4.5	4.5	3	12.5	26	2.3	68
7	M.a.	E	4	4.5	4.5	2.5	7	26	2.5	85
8	C.s.	W	2.5	5.0	5.0	5	10	44		65
9	C.s.	NW	1.5	5.0	4.5	4	9.5	32	2.3	65
10	C.s.	E	2.0	6.0	6.0	9	10	48		115
11	C.s.	NW	1.4	5.0	4.5	4	8	38	2.0	66
12	Cer.s.	W	2.3	4.5	4.5	3	10	39	1.8	62
13	K.p.	SW	2.2	4.6	5.0	3	10	30	1.5	120
14		S	3.5	4.5	4.5	6	9	32	1.6	100
15	E.c.	N	1.2	6.0	6.0	4	11	46	2.7	64
16	A.c.	N	1.5	5.0	5.0	6	9	35	1.1	65
17	M.n.	S	1.7	4.0	5.0	3	10	26	2.5	140
18	C.p.	NE		5.0	4.5	3	15	26	2.9	
19	P.d.	SSE		5.0	5.0	1.5	14.5	23	3.3	
Mean ± S.D.			2.1 ± 0.8	5.0 ± 0.5	4.8 ± 0.5	4.6 ± 2.2	9.9 ± 2.2	34.5 ± 7.7	2.2 ± 0.6	82.0 ± 23.7

[a] Abbreviations: M.a. = *Melia azedarach*; C.s. = *Ceratonia siliqua*; Cer.s. = *Cercis silquastrum*; K.p. = *Kigelia pinnata*; E.c. = *Eucalyptus camaldulensis*; A.c. = *Acacia cyanophila*; M.n. = *Morus nigra*; C.p. = *Carya pecan*; P.d. = *Peltophorum dubium*.

Table 2

Ambient and occupied cavities temperatures during various months of the year and average mean difference

Month of observation	Inhabitants (adult + nestlings)	Ambient temperature (°C)			Nest temperature (°C)			Average Δ temperature (°C)
		Min	Max	Average	Min	Max	Average	
January	1 + 0	2	14	10.8	7	22	15.1	4.3
February	1 + 0	9	19	16.2	12	22	18	1.8
February	1 +0	4	19	13.1	8	23	17.2	4.1
May	1 + 2 or more	21.1	26.3	23.5	27.1	30	28	4.5
May	1 + 2 or more	19.8	24.2	21.6	25.2	28.4	26.8	5.2
June	0 + 2 or more	19.5	25	22.8	24	28.4	26.2	3.4
June	0 + 3	20.4	30.1	23.4	26.9	40	32.9	9.5
June	0 + 1	23	25.9	23.6	25.9	30.4	27	3.4
July	1 + 0	18	24	22.7	21	27	25.7	3
September	1 + 0	19	24	23.6	23	28	27.5	3.9
November	1 + 0	3	16	11.5	6	25	15.5	4
Overall average ± S.D.								4.3 ± 1.9 ($N = 11$)

Table 3

Cavities O_2 conductance ($G_{\mathrm{NO_2}}$) values calculated under different conditions of wind speeds and directions at the opening of the artificial cavity

Wind speed range (m/s)	$G_{\mathrm{NO_2}}$ (ml$_{\mathrm{[STPD]}}$ (Torr h)$^{-1}$)			
	Frontal wind	Side wind	P	Averaged $G_{\mathrm{NO_2}}$
0.06–0.13	21.5 ± 5.43 (7)	17.6 ± 2.67 (6)	NS	19.7 ± 4.68 (13)
0.17–0.30	24.2 ± 2.67 (7)	39.9 ± 1.92 (6)	*	
0.33–0.47	57.0 ± 10.3 (7)	68.1 ± 1.82 (6)	**	
0.72–0.82	77.1 ± 5.41 (4)	73.1 ± 12.2 (6)	NS	74.7 ± 9.83 (10)
1.64–1.80	85.2 ± 7.51 (5)	80.3 ± 11.4 (5)	NS	82.8 ± 9.47 (10)

Values are mean ± S.D. Sample sizes are in brackets. NS: not significant.

* $P \ll 0.0005$.

** $P = 0.025$.

provides mean $G_{\mathrm{NO_2}}$ values calculated for each wind speed and direction. $G_{\mathrm{NO_2}}$ values for a side wind in the range of 0.17–0.30 and 0.33–0.47 m s^{-1} were significantly higher than the respective values for frontal wind (Student's t-test, Table 3). The effect of wind speed on $G_{\mathrm{NO_2}}$ appeared to be quite influential at lower wind speeds and leveled off at higher ones, for both frontal and side winds. Fig. 3 shows these wind effects on $G_{\mathrm{NO_2}}$ at the cavity opening and the corresponding equations.

Effect of heat convection on $G_{\mathrm{NO_2D}}$. At T_A of 18.1 ± 0.6 °C, $G_{\mathrm{NO_2}}$ was found to be 27.2 ± 5.9 ml (Torr h)$^{-1}$ ($n = 6$). This value is 3.8 times the value for $G_{\mathrm{NO_2D}}$ without heating.

3.3. $\dot{M}_{O_2}$, $\dot{M}_{CO_2}$ and T_b of the Syrian woodpecker, measured in the laboratory

Fig. 4A and B shows the relationship between woodpecker $\dot{M}_{O_2}$ and T_A for day and night, respectively. Five woodpeckers, aged about 1.5 years, were used in these experiments. The average body mass of these woodpeckers was 63.0 ± 4.7 g. Lower and upper critical temperatures (LCT and UCT, respectively), that determine the TNZ, were found to be approximately 20 and 35 °C (see Fig. 4A and B). T_b at these TNZs were found to be 41.97 ± 0.12 °C ($n = 3$) and 40.13 ± 1.14 °C ($n = 3$) for day and night experiments, respectively.

Day $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ (in ml (g h)$^{-1}$) at TNZ ($n = 8$) were 3.49 ± 0.49, and 1.79 ± 0.26, respectively. Night values were 2.53 ± 0.26 and 1.31 ± 0.06, respectively. Both $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ at TNZ during the day were significantly higher than the respective values at night (One-tailed paired t-test, $t_7 = 1.89$ and $P < 0.001$ for both cases).

For all T_A ranges, RQ did not differ significantly between day and night (two-tailed unpaired t-test). There was no correlation between RQ and T_A. All data were pooled and averaged. Calculated RQ was found to be 0.54 ± 0.09.

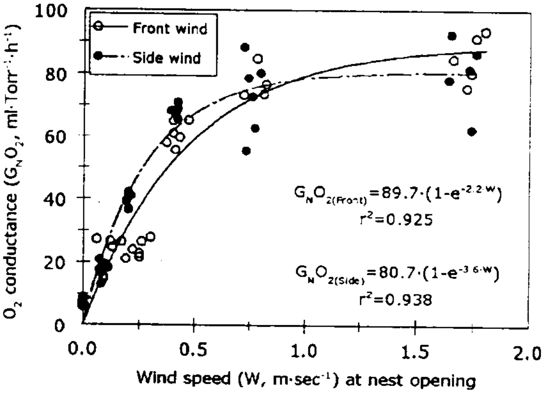

Fig. 3. The effects of frontal and side winds (m s^{-1}) at the opening of the artificial cavity on cavity O$_2$ conductance (G_{NO_2}; ml$_{[STPD]}$ (h Torr)$^{-1}$).

The calculated heat conductance values (C_b, expressed in units of ml (g h °C)$^{-1}$ of O$_2$, see Section 2) were 0.16 during the day and 0.14 at night. Accordingly, LCT for day and night were 20.0 and 22.3 °C, respectively. Day and night UCT could not be calculated with precision.

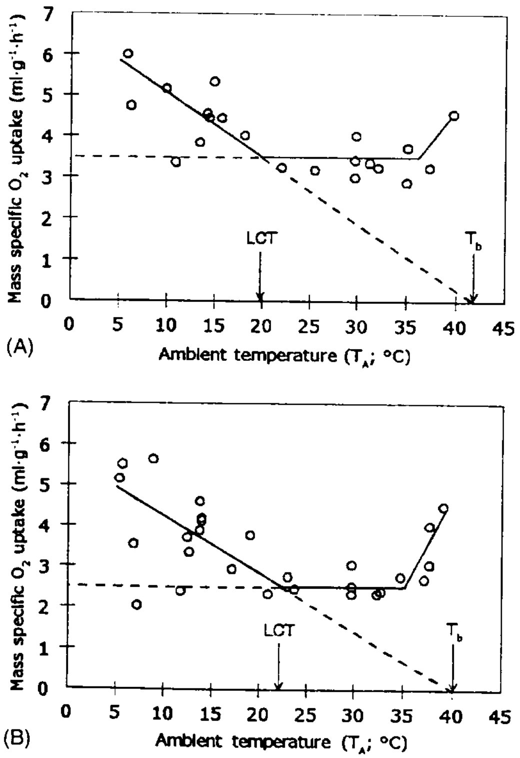

Fig. 4. The relationship between ambient temperature (T_A) and mass-specific O$_2$ uptake ($\dot{M}_{O_2}$) of a woodpecker, for day (A) and night (B). LCT = lower critical temperature.

4. Discussion

4.1. Natural cavity properties: advantages and disadvantages in cavity dwelling

Minimal nest depth was approximately the same as the woodpecker's body length. However, some of the cavities were twice as deep (Table 1). We do not have sufficient data to classify the cavities as either nesting or sleeping ones, but it is intriguing to suggest that the shallower ones are for sleeping of a single bird. The distribution of cavity depths was not Gaussian, and 11 of the 19 cavities sampled were in trunks and limbs of two species with soft timber. The mean entrance diameter and the horizontal corridor leading to the vertical cavity (Fig. 1) also seem to be the minimal possible for a woodpecker to pass through, probably to eliminate invasion and to save excavation. Since our observations indicate that woodpeckers always leave the cavity head first, cavity diameter is somewhat wider, probably to allow the woodpecker to turn around and in order to accommodate the eggs and the incubating bird.

Frontal cavity wall thickness was on the average only 4.6 cm, although the overall average tree diameter was 26.1 cm. This, together with the fact that the preferred entrance orientation is facing sunrise (Fig. 2), suggests that nest orientation may play a role in warming the cavity after a cold night.

The fact that Syrian woodpeckers dwell in their cavities all year round at night-time, seems advantageous. Some of the advantages of cavity dwelling, and in particular nesting, seem obvious and have been discussed before. For example, cavities are thought to protect inhabitants from predators (Gill, 1990). In addition, it has been shown that excavators have a significantly greater nesting success rate than non-excavators, with woodpeckers having the highest average rate of success (Johnson and Kermott, 1994).

Another possible advantage is the protection from weather conditions: birds may benefit from thermoregulatory energy savings during year round roosting in a tree cavity. This has been previously reported for the house sparrow (Kendeigh, 1961), for the acorn woodpecker, *Melanerpes formicivorous* (Du Plessis et al.,

1994) and for the eastern phoebe, *Sayornis phoebe* (Weeks, 1994). Similarly, our results show that the temperature inside the occupied cavities is higher at night than the ambient temperature by an average of 4.3 °C (Table 2). This is advantageous especially during long, cold winter nights for the adults and for both offspring and adults during the breeding season (April–June; Barnea, 1982). This will be further discussed below.

Possible disadvantages, in particular those that are related to gas exchange, have been seldom investigated in birds (Wilson and Kilgore, 1978; White et al., 1978; Wickler and Marsh, 1981; Howe and Kilgore, 1987; Howe et al., 1987; Ar, 1992; Ar and Piontkewitz, 1992). If a hypoxic-hypercapnic atmosphere develops in such cavities, it must be counteracted by either physiological or behavioral adaptations (Ar, 1992). From the point of view of behavior, it is interesting to note that woodpeckers spend longer time at nights (by about 1 h per day) in their cavities, as compared to other day-time active birds (Barnea, 1982). However, before investigating thermal properties of the cavity, it is important to establish whether the Syrian woodpecker encounters hypoxia in its cavity. This requires the detailed knowledge of rates of oxygen consumption of the woodpecker under different thermal conditions.

4.2. Oxygen consumption rate and thermal conditions

Steady-state oxygen consumption rates at rest of the woodpeckers were significantly different between day and night times (Fig. 4A and B). This is similar to the general trend found in birds. However, both day and night values were significantly higher, approximately double the allometrically predicted values for basal metabolic rates (BMR) calculated from Aschoff and Pohl (1970). This can be partially explained by the fact that our birds were not in complete 'post-absorptive state' as required for BMR measurements and presumably not always in complete rest.

The lower than expected RQ found in these woodpeckers (average 0.54; ranging from 0.37 to 0.72) attracted our attention. We double-checked the set-up physically, its calibrations, and our calculations. We found no evidence for possible error in the results of the measurements. Birds were allowed enough time to recover from hyperventilation and hyperthermia due to struggling before measurements started (see Section 2). Thus, CO_2 retention during measurements is ruled out. If true, then the results may indicate that, given their diet (rich in proteins and fat and poor in carbohydrates), the birds may have used in part the metabolic paths of gluconeogenesis and ketogenesis (Schutz and Ravussin, 1980).

Day and night thermal conductance values for the woodpecker in laboratory measurements were 30 and 80% higher respectively than the predicted values calculated from Aschoff (1981). These high conductance values are associated with the relatively low LCTs of the woodpeckers. These temperatures of approximately 20 and 22 °C for day and night, respectively, are lower than the predicted LCTs of a typical non-passerine bird of the same mass (27–29 °C for day and 22–24 °C for night, as calculated from the equations given by Aschoff and Pohl (1970) and Aschoff (1981)). The high conductance values can be explained by the higher than predicted BMRs found in woodpeckers as mentioned above. In addition, Table 2 shows that the temperature inside the cavity at night is, on the average, 4.3 °C higher than ambient temperature, due to the presence of a single woodpecker or more inside. This means that effectively the night LCT of the woodpecker in the cavity is lowered to an average ambient temperature of $22.3 - 4.3 = 18.0\,°\mathrm{C}$, and thus corresponds to a saving in energy of $4.3\,°\mathrm{C} \times 0.14\,\mathrm{ml}\,(\mathrm{g}\,°\mathrm{C}\,\mathrm{h})^{-1} = 0.61\,\mathrm{ml}\,(\mathrm{g}\,\mathrm{h})^{-1}$ in oxygen units, which are equivalent to ~24% of the woodpecker's resting metabolic rate at the TNZ at night (0.14 is the C_b value at night, see Section 3). The calculated heat conductance of the cavity itself when holding one woodpecker in its TNZ at night is $0.59\,\mathrm{ml}\,(\mathrm{g}\,\mathrm{h}\,°\mathrm{C})^{-1}$ which corresponds (not surprisingly) to about 24% of the woodpecker body resistance to heat loss (inverse of C_b). Du Plessis and Williams (1994) and Du Plessis et al. (1994) have calculated similar energy saving in cold nights for various temperature differences between the cavity and ambient for roosting green woodhoopoes and acorn woodpeckers. However, their calculations were not based on the energy saving at the lowered night LCT. It is interesting to note that a similar value of 27% was also obtained from theoretical considerations for closed nests in general (Ar and Sidis, 2001). For the cliff swallow, Withers (1977) found a difference of 0–7 °C between the occupied nest and ambient air, and Howe et al. (1987) indicated in the northern flicker that the temperature difference fluctuates between day and night due to a lag in the tree diel cycle.

4.3. Mathematical model of oxygen pressure in the cavity

A mathematical model that describes the partial pressure of oxygen in a nest cavity has already been advanced for the bee-eater by Ar and Piontkewitz (1992). However, that model was developed for steady-state conditions and did not take into account dynamic changes in the rate of oxygen pressure in the cavity with time. To account for dynamic changes, such as the change with time in $P_{\mathrm{NO_2}}$ from that of ambient air in an empty cavity to a steady-state once it has been inhabited by a woodpecker, the following mathematical model has been established:

$$P_{\mathrm{NO_2}(t_i)} = P_{\mathrm{NO_2}(t=0)} - [m \cdot (1 - \mathrm{e}^{(-G_{\mathrm{NO_2}} t_i)})]. \qquad (3)$$

Symbols are as in Eq. (1), t_i is any time from entering the nest cavity ($t = 0$) and m is the sum of the rates of oxygen consumption of all the nest cavity inhabitants converted into pressure units ($\Sigma \dot{M}\mathrm{O_2}$, in units of mol RT h^{-1}) divided by the nest cavity oxygen conductance ($G_{\mathrm{NO_2}}$).

Fig. 5 illustrates the time course for establishing steady-state $P_{\mathrm{NO_2}}$ from the moment a woodpecker enters into its cavity. The curves given are for oxygen diffusion alone (using $G_{\mathrm{NO_2D}}$), diffusion and heat convection (using $G_{\mathrm{NO_2(D+H)}}$), and the combined influence of diffusion, heat convection and wind velocity above 1.5 m/s ($G_{\mathrm{NO_2(W+D+H)}}$). Howe and Kilgore (1987) did not find any thermal influence on gas diffusive exchange in the cavity, when temperature in it exceeded by 5 °C that of the outside. In contrast to this finding, the effect of heat convection on gas exchange (presumably ~4.0 to 4.5 °C) for our model, was to increase steady-state $P_{\mathrm{NO_2}}$ by ~20 Torr. Wind has a strong effect on $G_{\mathrm{NO_2}}$ (Fig. 3). Nevertheless, as can be seen from Fig. 5, the effect of wind is relatively small as compared to that of heat convection. Thus, surprisingly, the model shows that wind (which is an unpredictably variable in field conditions) has relatively little effect on the gas composition in the cavity bottom of an occupied nest. This is in contrast with Facemire et al. (1990) who suggest that nest cavity ventilation provides a constant environment for the occupants. The solid line in Fig. 5 shows that the presence of a woodpecker plus three mature offspring may pose a problem since the atmosphere in the cavity becomes significantly hypoxic.

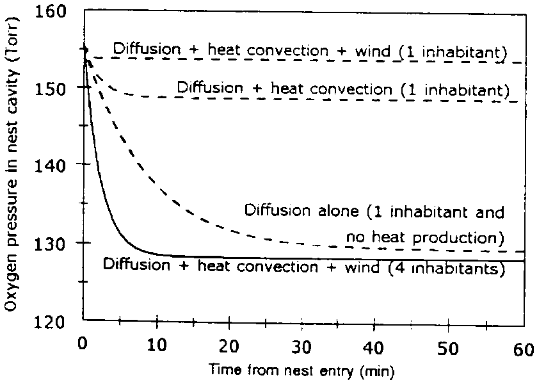

Fig. 5. Calculated oxygen pressure in the cavity as a function of time from the moment a woodpecker enters its cavity. Dashed curves are for one inhabitant with: oxygen diffusion alone; diffusion and heat convection; combined effect of diffusion, heat convection and wind. The solid line is for a woodpecker plus three mature offspring with the combined effect of diffusion, heat convection and wind.

In conclusion, our results and model show that, on average, a single woodpecker, outside the breeding season, staying in its cavity at night, does not encounter significant hypoxic conditions. However, the model indicates that during the breeding season, with more inhabitants consuming oxygen, with oxygen conductance of the nest cavity below the average, and when no wind is present, hypoxic conditions may develop in the nest cavity. This problem may be solved by physiological and/or behavioral adaptations. In the absence of concrete physiological findings in the literature, our field and laboratory observations (Barnea, 1982; Mersten-Katz, 1997b) indicate a possible behavioral adaptation: woodpeckers have been found to move up and down in their cavities at night, at various time intervals. Between vertical movements, the birds stayed at the bottom of their cavities. We hypothesize that when performing these vertical movements, the woodpecker acts as a piston, ventilating the cavity. To test this hypothesis thoroughly, additional data on natural nest cavities during the breeding season at nights are being gathered.

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