

EXERCISING WITH AND WITHOUT LUNGS

I. THE EFFECTS OF METABOLIC COST, MAXIMAL OXYGEN TRANSPORT AND BODY SIZE ON TERRESTRIAL LOCOMOTION IN SALAMANDER SPECIES

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Summary

Metabolic cost, oxygen consumption (\dot{M}_{O_2}), respiratory structure and body size interact to determine the capacity of salamanders for terrestrial locomotion. Salamanders respiring *via* both lungs and skin, *Ambystoma laterale* and *A. tigrinum*, or with skin alone, *Desmognathus ochrophaeus* and *D. quadramaculatus*, attained a steady-state \dot{M}_{O_2} during exercise in a treadmill respirometer. Endurance was correlated with the speed at which maximal \dot{M}_{O_2} was attained ($v_{M_{O_2,max}}$). Low aerobic costs of transport (60–80% lower than reptiles of similar mass) increased $v_{M_{O_2,max}}$. However, in lungless salamanders a low maximum \dot{M}_{O_2} decreased $v_{M_{O_2,max}}$ significantly. \dot{M}_{O_2} increased only 1.6- to 3.0-fold above resting rates in active lungless salamanders, whereas it could increase 3.5- to 7.0-fold in active lunged salamanders. Lungless salamanders attained maximal \dot{M}_{O_2} at half to one-tenth the speed of lunged animals. Lungless salamanders fatigued in 20 min or less at speeds that lunged salamanders could sustain for 1–2 h. Body size also affected the capacity for oxygen uptake during activity and locomotor performance. The large lungless salamander *D. quadramaculatus* attained maximum \dot{M}_{O_2} even at its lowest rate of travel. Cutaneous gas exchange does not provide lungless salamanders with gas transport capacities found in lunged animals. However, only small increases in \dot{M}_{O_2} may be required for modest levels of activity.

Introduction

A major issue in the analysis of vertebrate, cutaneous gas exchange is the extent to which skin-breathing can be regulated (Feder & Burggren, 1985*a,b*), especially in the face of an increasing gas exchange requirement, such as occurs during exercise. Examination of this issue is often complicated because cutaneous respiration usually occurs in combination with pulmonary respiration, branchial

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respiration or both; attribution of an experimental result to cutaneous gas exchange alone is often impossible. However, adult plethodontid salamanders lack lungs and gills, and thus their skin and buccopharyngeal lining are the sole sites of gas exchange. Because plethodontid salamanders otherwise resemble their lunged counterparts, salamanders are an ideal group of subjects for comparative studies of the efficacy of cutaneous gas exchange.

Diffusion appears to limit cutaneous oxygen uptake even in resting lungless salamanders (Gatz *et al.* 1975; Piiper *et al.* 1976). This diffusion limitation is due in large part to the thickness of the skin overlying the cutaneous respiratory capillaries (Czopek, 1965), which is much thicker than the diffusion barrier in the lungs or gills of most vertebrates (Feder & Burggren, 1985a). Moreover, diffusion limitation of oxygen transport should become even more severe when oxygen demand increases during activity (Feder *et al.* 1988). Reliance on cutaneous respiration during locomotion could severely limit the maximal rate of oxygen consumption ($\dot{M}_{O_2, \max}$), reduce the speed attained at $\dot{M}_{O_2, \max}$ ($v_{M_{O_2, \max}}$), and decrease endurance because of an inability to adjust oxygen uptake to changing muscle demands. Furthermore, because both cutaneous surface area and skin thickness scale allometrically with body mass in salamanders (Czopek, 1965), increasing body size should exacerbate diffusion limitation and its consequences, especially in active salamanders.

In contrast, recent studies of skin-breathing amphibians have suggested ways in which cutaneous gas exchange might be regulated despite a large diffusion limitation (Feder & Burggren, 1985a). In particular, vertebrates may control capillary recruitment in response to hypoxia and hypercapnia and thereby adjust cutaneous diffusing capacity (Feder & Burggren, 1985b; Burggren & Moalli, 1984). Also, because the diffusion limitation, although large (Gatz *et al.* 1975; Piiper *et al.* 1976), is not complete, changes in gross blood flow to the skin will have some effect on gas exchange, even in the absence of capillary recruitment (Malvin, 1988). Such adjustments might account for the activity capacity of some lungless salamanders. For example, Full (1986) demonstrated that the lungless salamander *Plethodon jordani* could increase oxygen consumption three- to nine-fold over standard rates during treadmill exercise. Moreover, Feder *et al.* (1988) found that the large skin-breathing salamander *Desmognathus quadramaculatus* could increase skin diffusing capacity during exercise to adjust to an increased oxygen requirement. These recent findings prompted our further examination of cutaneous gas exchange and its possible significance during locomotion. We selected two paths of investigation: (1) a comparative approach in which lunged and lungless species were tested under controlled conditions, and (2) direct experimental manipulation altering lunged salamanders so that they became functionally lungless (Feder, 1988).

The present study focuses on the first approach. Previous research has characterized resting oxygen consumption, 'maximal' aerobic metabolism and recovery oxygen uptake (Bennett & Licht, 1973; Feder, 1976, 1977; Hillman *et al.* 1979; Whitford & Hutchison, 1967; Withers, 1980). Withers (1980) measured a

four-fold increase in the oxygen consumption during 3 min of repeated flipping in plethodontids, ranging in size from 0.5 to 6 g. Allometric analyses indicated that cutaneous surface area of large plethodontid salamanders might limit their maximal aerobic metabolic rate and maximal attainable body mass. These studies imply that natural activity, such as locomotion, is limited by cutaneous gas exchange, especially in large animals.

Unfortunately, no previous study of the effects of lunglessness and body size on activity has quantified exercise levels or directly related oxygen uptake to actual endurance. By using a treadmill we imposed a quantifiable exercise regime. To determine the constraints of lunglessness on locomotion we assessed the metabolic cost of locomotion, $\dot{M}_{O_2, \max}$, and endurance capacity as a function of speed and body mass.

Materials and methods

Animals

We used four species of salamanders: *Desmognathus ochrophaeus* and *Desmognathus quadramaculatus*, which lack lungs, and *Ambystoma tigrinum* and *Ambystoma laterale*, which have lungs. The larger salamanders, *D. quadramaculatus* and *A. tigrinum*, were of similar mass (Table 1). Of the smaller salamanders, *D. ochrophaeus* was less than half the mass of *A. laterale*. *D. quadramaculatus* and *A. tigrinum* were an order of magnitude greater in body mass than *D. ochrophaeus* and *A. laterale*.

D. ochrophaeus and *A. laterale* were captured near Highlands, North Carolina and Lincolnshire, Illinois, respectively. Commercial suppliers provided the *D. quadramaculatus* and *A. tigrinum*. All animals were maintained at 12–14°C on a 14 h:10 h light:dark photoperiod centred at 13.00 h local time. *Desmognathus ochrophaeus* were fed fly larvae, whereas other species were fed corn grubs. All animals were fed weekly until 3 days before metabolic or endurance measurements. Individuals were exposed to the experimental temperature (21°C) at least 1 h before measurements. We selected an experimental temperature of 21°C based on pilot studies of overall locomotor performance.

Oxygen consumption

Oxygen consumption was measured in airtight Lucite respirometers containing a variable-speed treadmill. Animals were rested on the treadmill under dim light for a minimum of 1 h before measurements were taken. Open-flow respirometry was used to measure the rate of oxygen consumption (\dot{M}_{O_2}) continuously during rest (minimum of 15 min) and exercise (20 min). The speeds for each species ranged from a slow speed that animals could sustain for more than 2 h, to a speed above their maximal oxygen consumption ($\dot{M}_{O_2, \max}$), at which fatigue occurred in less than 20 min. Speeds were evenly divided to give 5–6 test speeds for each species. Animals were run only once a day at a single speed and were given a

minimum of 1 day between trials. Experiments in which animals did not run consistently were discarded.

Humidified air was drawn through the chamber at a constant flow rate (\dot{V}) determined by a flow meter. The air leaving the chamber was drawn through a column containing CaSO_4 (Drierite) and Ascarite to remove H_2O and CO_2 from the air, respectively. The incurrent fractional oxygen concentration (F_I) was compared with the excurrent fraction (F_E) by a dual-channel oxygen analyser (Ametek Applied Electrochemistry, model S-3A). The oxygen analyser was interfaced with an analogue to digital converter (Isaac 41A System, Cyborg Inc.) and a microcomputer (Apple II⁺). Averaging and N -point smoothing ($N=3$) were employed to remove the noise found in control tests during which O_2 concentration was held constant.

Instantaneous \dot{M}_{O_2} was calculated from F_I and F_E . Given any two measurements separated by a brief interval and the 'washout' characteristics of the chamber, F_{EQ} (the equilibrium of F_E inside the metabolic chamber) can be calculated and substituted for F_E in a standard equation:

$$\dot{M}_{\text{O}_2} = \dot{V}(F_I - F_{EQ})/(1 - F_I)$$

to estimate instantaneous \dot{M}_{O_2} (Full, 1986; Herreid *et al.* 1981). Different chamber sizes and gas flow rates were used to accommodate the varying size and O_2 consumption of the four species. Flow rates for *D. ochrophaeus*, *D. quadramaculatus*, *A. laterale* and *A. tigrinum* were 20, 75, 50 and 350 ml min⁻¹, respectively; effective volumes were 59, 321, 168 and 1100 ml, respectively. The 'effective volume' used in the calculation of F_{EQ} was calculated from the washout of a standard gas mixture (20.850% O_2 , balance N_2). All values were converted to μmol .

Endurance capacity

Salamanders were exercised to fatigue inside the humidified treadmill respirometer after a rest period of at least 10 min. Each trial was performed at a single speed. A range of speeds was chosen for each species. This range included slow speeds at which the animal could run for an arbitrary 2 h time limit and fast speeds at which the animal fatigued in under 5 min. The animals were periodically prodded with a rigid wire when they did not move at constant speed. Frequent prodding became necessary just before fatigue. Fatigue was defined as that time when an animal (1) did not maintain pace with the treadmill, (2) dragged its abdomen, and (3) did not respond to three successive prodding attempts (Full, 1986). Animals were run only once a day and were given a minimum of 2 days between trials. Trials in which animals did not walk consistently were discarded.

Statistical methods

We used standard least-squares regression to determine the relationship between oxygen consumption and speed, as well as endurance and speed. Each function was tested for linearity. To examine the effects of lunglessness, we used

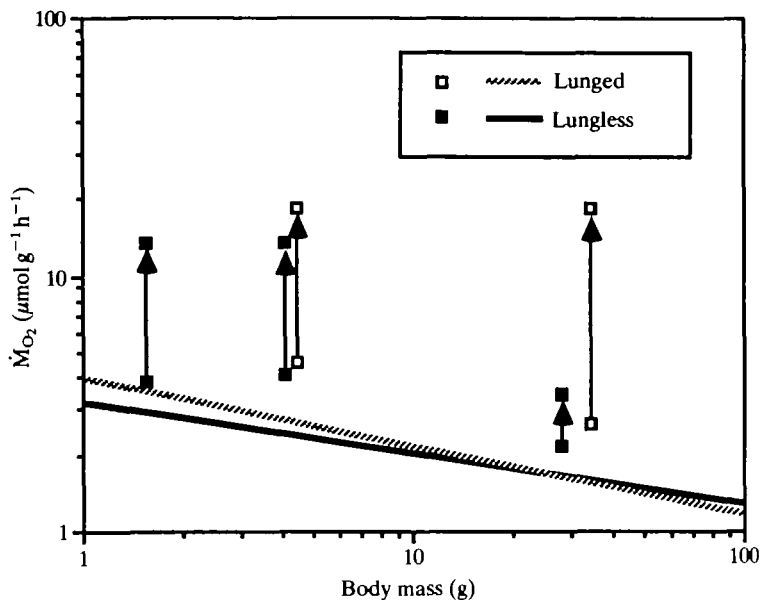


Fig. 1. Mass-specific resting and maximal oxygen consumption (\dot{M}_{O_2}) of lunged and lungless salamanders as a function of body mass. Regression lines represent standard oxygen consumption data (corrected to 21°C assuming $Q_{10} = 2$) from Feder (1976). Symbols at the origin of an arrow indicate resting \dot{M}_{O_2} measured in the present study or in Full (1986); symbols near the arrowhead represent maximal \dot{M}_{O_2} .

an analysis of covariance (ANCOVA) with either body mass or speed as the covariate (Systat Inc.). Homogeneity of slopes was tested to determine whether a significant interaction existed between the covariate and treatment.

Results

Oxygen consumption

Resting mass-specific oxygen consumption ($\dot{M}_{O_2,rest}$) decreased with body mass ($F_{(1,35)} = 5.1$, $P = 0.03$; Fig. 1). Lunglessness did not affect $\dot{M}_{O_2,rest}$ (ANCOVA, $F_{(1,33)} = 2.5$, $P = 0.12$). The mean $\dot{M}_{O_2,rest}$ for each species was greater than standard rates reported by Feder (1976), who acclimated animals for 1 week. These results are typical and probably due to handling.

The \dot{M}_{O_2} of all salamanders approached a steady-state (designated $\dot{M}_{O_2,ss}$) within 5 min of the start of exercise. The rate of increase in \dot{M}_{O_2} of animals that performed flawlessly from the start of treadmill exercise was comparable with that reported for *P. jordani* (see fig. 1 in Full, 1986, for patterns typical of salamanders). However, in some cases \dot{M}_{O_2} increased less rapidly when animals did not initially keep pace with the treadmill. In other cases, \dot{M}_{O_2} exceeded the steady-state rate momentarily when salamanders resisted walking.

Energetic cost of locomotion

Steady-state oxygen consumption ($\dot{M}_{O_2,ss}$) increased linearly with speed in *A. laterale*, *A. tigrinum* and *D. ochrophaeus* (stepwise polynomial regression analysis, $P < 0.05$; Table 1; Fig. 2). $\dot{M}_{O_2,ss}$ and speed were not related in *D. quadramaculatus* (Table 1).

Minimum cost of locomotion – slope

Body mass. The largest salamander, *A. tigrinum*, had the lowest mass-specific C_{min} (the slope of the $\dot{M}_{O_2,ss}$ versus speed function which represents the minimum cost used to travel a given distance), whereas the two smaller species, *A. laterale* and *D. ochrophaeus*, had significantly higher costs (ANCOVA with Bonferroni procedure for *post hoc* analysis, $P < 0.001$; Fig. 3). Calculation of C_{min} for *D. quadramaculatus* was impossible because $\dot{M}_{O_2,ss}$ did not increase with speed. Anaerobic metabolism almost certainly supplemented aerobic energy production as speed increased. The best estimate of the cost of locomotion for *D. quadramaculatus* is the net cost of transport [$C_{net} = (\dot{M}_{O_2,ss} - \dot{M}_{O_2,rest})/\text{speed}$] at $v_{M_{O_2,max}}$, where aerobic metabolism probably contributed the majority of energy. Even though C_{net} is not a minimum cost, estimations of C_{net} ($32 \mu\text{mol g}^{-1} \text{km}^{-1}$) for the large *D. quadramaculatus* were lower than costs in small animals (Fig. 2).

Lunged vs lungless salamanders. No effect of lunglessness on C_{min} could be demonstrated. Differences in C_{min} could not be determined between the larger lunged and lungless species because the C_{min} of *D. quadramaculatus* was not significantly different from zero. No difference was detected in C_{min} between the smaller lunged and lungless species, *A. laterale* and *D. ochrophaeus*, despite a 2.8-fold difference in body mass ($F_{(1,31)} = 1.17$, $P = 0.29$). Yet, in animals of similar body mass but with and without lungs (*A. laterale* and *P. jordani*) the C_{min} was lower in the lunged species ($F_{(1,38)} = 18.6$, $P < 0.001$).

y-intercept

Body mass. Body mass had no significant effect on the y-intercept of the $\dot{M}_{O_2,ss}$ versus speed function (Table 1). *D. quadramaculatus* and *A. tigrinum*, the largest animals, accounted for both the lowest (3.6) and highest values (11.2), respectively.

Lunged vs lungless salamanders. The y-intercept was considerably higher in *A. tigrinum*, the largest lunged animal, compared with *D. quadramaculatus*, the lungless species of comparable size. In fact, the y-intercept/ $\dot{M}_{O_2,rest}$ ratio of *A. tigrinum* was 2- to 6-fold greater than in the other species tested. The y-intercept was not significantly different in *A. laterale* and *D. ochrophaeus*, the smaller animals ($F_{(1,32)} = 0.53$, $P = 0.47$).

*Maximal oxygen consumption**Body mass*

Mass-specific $\dot{M}_{O_2,max}$ did not decrease predictably with body mass (Fig. 1; Table 1). Surprisingly, *A. tigrinum*, the largest animal, had the highest mass-

Table 1. Aerobic metabolism of lunged and lungless salamanders during rest and exercise

Species	Body mass (g)	$\dot{M}_{O_2,rest}$ ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$)	$\dot{M}_{O_2,ss}$ ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$) vs speed (v, km h^{-1})	y-int/ $\dot{M}_{O_2,rest}$	$\dot{M}_{O_2,max}$ ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$)	$\dot{M}_{O_2,max}/\dot{M}_{O_2,rest}$	$v_{M_{O_2,max}}$ (km h^{-1})
Lunged							
<i>Ambystoma laterale</i>	4.4 ± 0.17	4.51 ± 0.62 (N = 12)	$\dot{M}_{O_2,ss} = 46.4v + 9.1$ (N = 19; $r^2 = 0.76$; $P < 0.001$)	2.01	18.5	4.1	0.200
<i>Ambystoma tigrinum</i>	34.2 ± 0.93	2.66 ± 0.35 (N = 5)	$\dot{M}_{O_2,ss} = 13.7v + 11.2$ (N = 18; $r^2 = 0.42$; $P = 0.004$)	4.21	>18.3	>6.9	>0.54
Lungless							
<i>Desmognathus ochrophaeus</i>	1.56 ± 0.052	3.80 ± 0.32 (N = 12)	$\dot{M}_{O_2,ss} = 70.7v + 5.81$ (N = 23; $r^2 = 0.46$; $P < 0.001$)	1.53	13.4	3.5	0.110
<i>Plethodon jordani</i> *	4.1 ± 0.010*	4.07 ± 0.24* (N = 30)	$\dot{M}_{O_2,ss} = 100.4v + 2.91$ * (N = 30; $r^2 = 0.84$; $P < 0.001$)	0.71	13.4*	3.3	0.100*
<i>Desmognathus quadramaculatus</i>	28.0 ± 0.51	2.16 ± 0.21 (N = 12)	$\dot{M}_{O_2,ss} = -2.03v + 3.62$ (N = 32; $r^2 = 0.01$; $P = 0.56$)	1.68	3.43	1.6	<0.043

Values are ± 1 s.e.

* Data from Full (1986) corrected to 21 °C assuming a Q_{10} of 2.

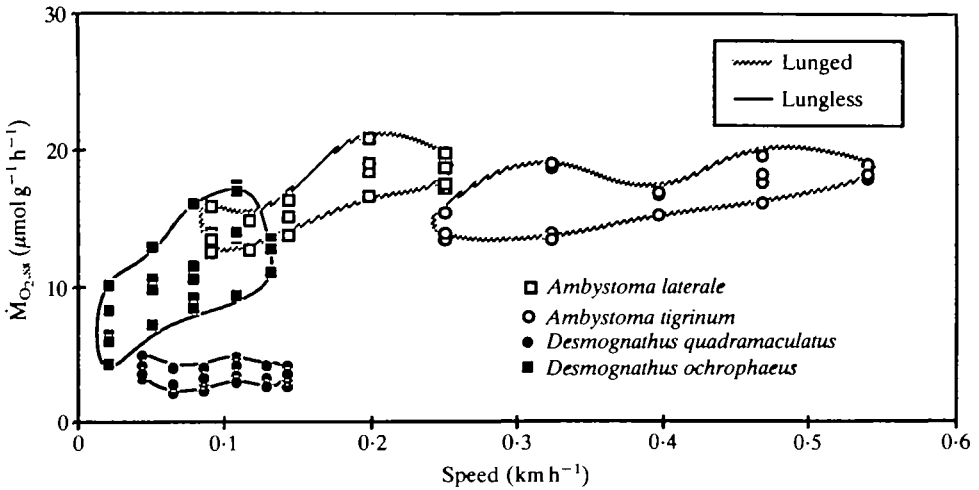


Fig. 2. Steady-state oxygen consumption ($\dot{M}_{O_2,ss}$) as a function of speed for lunged and lungless salamanders. *Desmognathus ochrophaeus* and *Ambystoma laterale* are of similar mass, as are *D. quadramaculatus* and *A. tigrinum*.

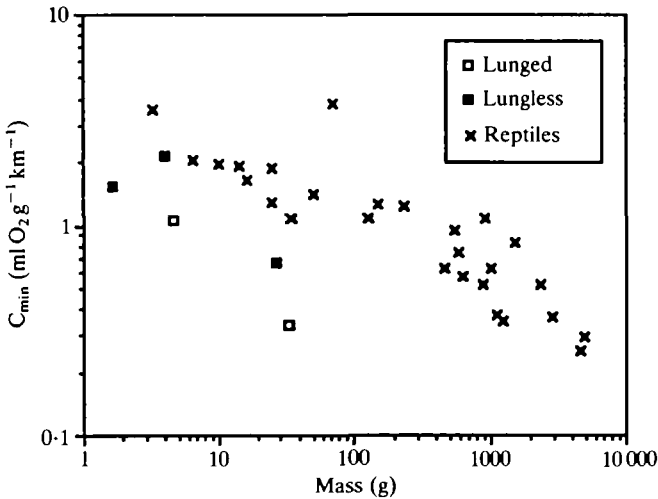


Fig. 3. Mass-specific, minimum cost of locomotion (C_{min}) as a function of body mass for lunged salamanders, lungless salamanders and lizards. Value for *Desmognathus quadramaculatus* (largest lungless animal) represents the net cost of locomotion [$C_{net} = (\dot{M}_{O_2,ss} - \dot{M}_{O_2,rest}) / \text{speed}$] not the minimum value. Data for lizards are from various sources as listed in John-Alder *et al.* 1986.

specific $\dot{M}_{O_2,max}$. This is in contrast with the scaling in birds, mammals and reptiles where mass-specific $\dot{M}_{O_2,max}$ decreases with body mass (Bennett, 1982; Taylor *et al.* 1980).

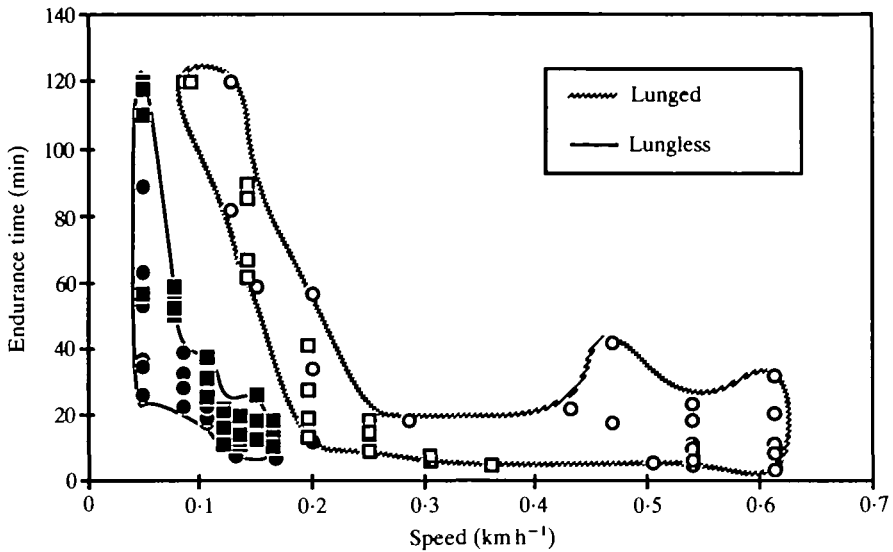


Fig. 4. Treadmill endurance (time to fatigue) as a function of speed for lunged and lungless salamanders. Each data point represents a separate trial. Experiments were terminated after 120 min of exercise if fatigue did not occur.

Lunged vs lungless salamanders

Lunged salamanders had a significantly greater $\dot{M}_{O_2,max}$ than lungless species (ANCOVA, $F_{(1,32)} = 95.9$, $P < 0.001$; Fig. 1). The factorial aerobic scope ($\dot{M}_{O_2,max}/\dot{M}_{O_2,rest}$) was also higher in the lunged species (Table 1).

Speed at $\dot{M}_{O_2,max}$

Body mass

The speed at which $\dot{M}_{O_2,max}$ was attained ($v_{M_{O_2,max}}$) was unrelated to body mass (Fig. 2; Table 1). The largest lunged species, *A. tigrinum*, had a greater $v_{M_{O_2,max}}$ than the smallest lunged species, whereas the largest lungless salamander, *D. quadramaculatus*, actually had a lower $v_{M_{O_2,max}}$ than the smallest lungless one, *D. ochrophaeus*.

Lunged vs lungless salamanders

Lunged salamanders had a greater $v_{M_{O_2,max}}$ than the lungless species (Table 1).

Endurance capacity

Endurance capacity decreased significantly as a function of speed in all salamanders (Fig. 4; Table 2). Endurance was compared using an analysis of covariance on log-transformed data.

Table 2. *Treadmill endurance of lunged and lungless salamanders*

Species	N	Endurance time = av^b		r^2
		b	a	
Lunged				
<i>Ambystoma laterale</i>	15	-3.0 (± 0.59)	0.21	0.90
<i>Ambystoma tigrinum</i>	21	-1.1 (± 0.64)	5.58	0.40
Lungless				
<i>Desmognathus ochrophaeus</i>	25	-1.9 (± 0.32)	0.37	0.87
<i>Plethodon jordani</i> *	22	-1.7 (± 0.64)	0.63	0.59
<i>Desmognathus quadramaculatus</i>	26	-1.5 (± 0.33)	0.71	0.78

Endurance time or time to fatigue is in min.

v is the animal's speed in km h^{-1} .

N is the total number of endurance trials.

Values in parentheses are 95% confidence limits.

* Data from Full (1986).

Body mass

No obvious effect of body mass was evident among the lungless species. The larger lungless species, *D. quadramaculatus*, actually had lower stamina than the smallest salamander tested, *D. ochrophaeus* ($F_{(1,46)} = 1.83$, $P = 0.05$). The larger lunged species, *A. tigrinum*, had greater endurance than the smaller lunged species, *A. laterale* ($F_{(1,34)} = 6.18$, $P = 0.02$).

Lunged vs lungless salamanders

Lunged salamanders had a significantly greater endurance than lungless species, independent of body mass ($P < 0.001$).

Discussion

In the present study the capacity for sustained locomotion in salamanders depended on the interaction of metabolic cost and $\dot{M}_{\text{O}_2, \text{max}}$, as in other animals (Bennett & John-Alder, 1984; Full, 1986, 1987). Regardless of body size, lungless salamanders had a lower $\dot{M}_{\text{O}_2, \text{max}}$ and a more limited endurance than lunged species.

Energetic cost of locomotion

Both lunged and lungless salamanders had a relatively low C_{min} (i.e. the amount

of energy required to move 1 g of animal 1 km; Table 1). Values were 60–80 % lower than predicted for lizards, birds or mammals of comparable mass (Fig. 3; John-Alder *et al.* 1986; Taylor *et al.* 1982). C_{\min} values in the present study were considerably lower than the high values reported for *Bolitoglossa subpalmata* and *D. ochrophaeus* exercising in a rotating-wheel respirometer (Feder, 1987a,b). This discrepancy may be due to the small range of speeds examined in the rotating-wheel respirometer or a difference in mechanical work output.

Several phenomena may explain the low minimum cost of locomotion observed in the present study. If salamanders were using anaerobic sources at high speeds, then the total amount of energy required for locomotion would be underestimated. Underestimating energy cost at high speeds, but not at low speeds, tends to undervalue C_{\min} . However, anaerobic contributions at speeds near $v_{\dot{M}_{O_2, \max}}$ cannot completely explain the low C_{\min} values. The lungless species *P. jordani*, tested under conditions similar to the present study, also has a C_{\min} 20 % lower than predicted for other vertebrates (Taylor *et al.* 1982), but anaerobic metabolism contributed little to energy needs at submaximal speeds (Full, 1986).

C_{\min} may also appear to be low if the energetic cost of locomotion is unduly elevated at low speeds, possibly due to erratic locomotion or extraneous movements. An elevated y-intercept would be consistent with this explanation. Three of the four species in the present study, along with *P. jordani*, did not appear to have elevated y-intercepts (Table 1). Each species had a y-intercept to rest ratio comparable to that of other vertebrates (Paladino & King, 1979) and invertebrates (Full, 1987; Herreid, 1981; Herreid & Full, 1983). *Ambystoma tigrinum* is an exception and its relatively high y-intercept remains to be explained. An additional possibility is that fundamental differences exist within the muscles themselves, perhaps relating to the energy cost of force development (Taylor, 1985). John-Alder *et al.* (1986) suggest a similar explanation in a comparison of two lizards similar in morphology but differing in C_{\min} .

The relatively low metabolic cost of locomotion in salamanders favours an increased $v_{\dot{M}_{O_2, \max}}$, all else (i.e. y-intercept and $\dot{M}_{O_2, \max}$) being equal. Exercise powered by a greater percentage of aerobic metabolism is correlated with an increased endurance.

Maximal oxygen consumption

Lungless salamanders had a limited capacity to increase \dot{M}_{O_2} (Table 1). $\dot{M}_{O_2, \max}$ of *D. ochrophaeus* was only 50 % of that predicted for a reptile of a similar body mass at comparable temperatures (Bennett, 1982). In the larger *D. quadramaculatus*, $\dot{M}_{O_2, \max}$ was 80 % below the predicted rate for reptiles. The relatively low $\dot{M}_{O_2, \max}$ is probably not unique to the genus *Desmognathus*, since the lungless salamander *P. jordani* also had an $\dot{M}_{O_2, \max}$ 40 % lower than reptilian rates (Full, 1986). $\dot{M}_{O_2, \max}$ values of lunged salamanders were more comparable with the rates of anurans (Hillman & Withers, 1979) and reptiles (Bennett, 1982).

The present comparison is consistent with cutaneous diffusion as a major resistance to gas exchange during activity, especially in large lungless salamanders.

The arterial partial pressure of oxygen (P_{O_2}) of the lungless salamander *D. fuscus* at rest is estimated to be 13.3 kPa below that of air (Piiper *et al.* 1976). Mixing with venous blood in the heart results in an even lower P_{O_2} (i.e. 5.3 kPa) in blood perfusing the tissues (Piiper *et al.* 1976). A low driving force for diffusion into the tissues may limit oxygen transport during exercise when demand is increased. Regulation of cutaneous gas exchange by recruiting unperfused capillaries, or increasing the bulk flow of blood, does not provide lungless salamanders with gas transport capacities observed in lunged animals. This does not imply that regulation of cutaneous oxygen uptake is unimportant, but only that the resulting increase in \dot{M}_{O_2} is of relatively small magnitude compared with the increases in lunged salamanders.

$v_{M_{O_2,max}}$ and endurance capacity

Lungless salamanders attained $\dot{M}_{O_2,max}$ at very low speeds. A low $\dot{M}_{O_2,max}$ was the primary determinant of the low $v_{M_{O_2,max}}$ (Table 1). Lungless salamanders attained $\dot{M}_{O_2,max}$ at speeds half to one-fifth of the speeds measured in reptiles (Garland, 1982, 1983). Mammals attain $\dot{M}_{O_2,max}$ at speeds an order of magnitude faster than reptiles (Garland, 1982, 1983; Taylor *et al.* 1980).

Endurance of both lunged and lungless salamanders was highly correlated with their $v_{M_{O_2,max}}$ (Fig. 2). Studies on reptiles (Bennett & John-Alder, 1984; John-Alder & Bennett, 1981) and arthropods (Full, 1987; Full & Herreid, 1983) have found a similar correlation. Thus, lungless salamanders have remarkably limited endurance (Table 2). Over a 10-min period resulting in fatigue, lunged species sustained speeds 5–6-times faster than lungless ones. The specific cause of fatigue in lungless or lunged salamanders is unknown. Locomotion at speeds above $\dot{M}_{O_2,max}$ leads to accelerated glycolysis resulting in lactic acid formation. Conflicting data exist as to whether lactic acid is the primary cause of fatigue in amphibians (Fitts & Holloszy, 1976; Putnam, 1979). The data in Fig. 4, and previous work on *P. jordani* (Full, 1986), suggest that other agents, such as substrate depletion, are involved. In nearly every species, treadmill endurance declines significantly well before $\dot{M}_{O_2,max}$ is attained, and presumably before net lactic acid production becomes substantial.

Large size may further limit cutaneous oxygen uptake by limiting skin surface area and increasing skin thickness (Czopek, 1965; Ultsch, 1976; Withers, 1980). Even at the slowest speeds, the largest lungless species (*D. quadramaculatus*) was always at $\dot{M}_{O_2,max}$ (Fig. 2). The onset of fatigue was rapid at all except the slowest speeds. Despite being nearly 20 times smaller, the smallest lungless species (*D. ochrophaeus*) could walk at speeds nearly twice that of *D. quadramaculatus* before attaining $\dot{M}_{O_2,max}$. Results from previous studies on plethodontid salamanders exposed to hypoxia are also consistent with the hypothesis that body size limits respiratory surface area, and hence oxygen uptake (Ultsch, 1976; Withers, 1980).

Field data collected on lunged and lungless salamanders are consistent with laboratory measurements of locomotor capacity. Some lungless salamanders have minuscule home ranges (Semlitsch, 1983; Nishikawa, 1985). For example, the

average distance travelled between recaptures by *D. ochrophaeus* was only 0.4–0.7 m (Huheey & Brandon, 1973; Holomuzki, 1982). *D. quadramaculatus* have been observed to move even less (Brandon & Huheey, 1971). Likewise, in the lungless genus *Plethodon*, home range size decreases rather than increases with increasing body size (Nishikawa, 1985, 1986). Gas exchange limitations, as demonstrated for lungless salamanders during treadmill locomotion, may restrict movement in the field.

In contrast, *Ambystoma* migrate to ponds for breeding and can travel several hundred metres (Shoop, 1965). Semlitsch (1983) reported that a radioactively tagged *A. tigrinum* moved 162 m in a single night. These observations are consistent with the laboratory measurements of $\dot{M}_{O_2, \max}$ and endurance.

In conclusion, lungless salamanders appear to be limited in their capacity to increase oxygen consumption and meet the demands of active muscle. Metabolic cost, maximal oxygen uptake and body size combine to determine locomotor performance. Large body size can place further restrictions on activity. Regulation of cutaneous gas exchange does not provide lungless salamanders with gas transport capacities found in lunged animals. However, small increases in \dot{M}_{O_2} may be important to large animals to allow modest levels of activity.

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