slightly over the next 2 hours in both experimental and control groups. This rapid rate of adsorption was in contrast to that in the plaque assay, which required a minimum 1-hour inoculum adsorption period for maximum adsorption of virus. This difference suggests that the two systems may have different receptor sites and attachment mechanisms.

Vertical transmission of virus by attachment to sperm cells has obvious advantages for infection of any host, but particularly when the host is a species in which fertilization takes place externally and in flowing water. Without adsorption, virus particles released with gametes during spawning would be immediately diluted and flushed away by the water. Adsorption of virus to sperm could deliver the pathogen directly to the ovum, with the sperm acting as a vehicle for the entry of the virus into the egg. Because of dilution, adsorption of virus to sperm must occur very quickly—a requirement that our results indicate is met. We have also found that adsorption occurs efficiently over the range of temperatures from 1.5° to 18°C—approximately the temperature range preferred by salmonids for spawning. Our finding that IHN virus adsorbs to sperm from two genera known to be natural hosts for the virus suggests that this mechanism of transmission may occur in all host species.

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Energy Scaling in Marsupials and Eutherians

Abstract. *Marsupials have been shown to have basal metabolic rates below those of eutherian mammals. Now metabolic rates below thermoneutrality are found to be equivalent in both taxa. Two models are proposed to explain the observed metabolic patterns: in one, marsupials differ only in having reduced basal metabolic rates; in the other, the reduced marsupial basal metabolic rates combined with a reduced body temperature and elevated conductance. The metabolic costs of existence below thermoneutrality appear to be similar for both taxa. The difference in basal metabolic rate may be of energetic significance or merely a phylogenetic coincidence.*

The minimal resting metabolic rate within thermoneutrality (basal metabolism) of marsupial mammals has been shown to be 70 percent of the corresponding eutherian level at any body mass (*1, 2*). Marsupials also are considered to have lower body temperatures than eutherians (*1, 3*). These considerations led Dawson (*3*) to construct a model with the metabolism of marsupials at temperatures below thermoneutrality also being lower than eutherians (Fig. 1A). Our allometric analyses of measured metabolic rates below thermoneutrality indicate that the marsupials do not have reduced metabolic levels except within thermoneutrality and that a more accurate model is that depicted in Fig. 1B. Our analysis is consistent with the findings that the maximum rate of metabolism in marsupials and eutherians is similar in response both to cold (*4*) and to exercise (*5*) and that the daily energy expenditure in natural settings is similar in both taxa (*6*).

Dawson's model (*3*) (Fig. 1A) shows the well-documented reduction in basal metabolism of the marsupials and the lower body temperature; the latter is shown by *x*-intercepts: the line relating metabolism to air temperature intersects zero metabolism at a lower temperature in marsupials. The shallower slope of the marsupial line below thermoneutrality indicates a lower minimal thermal conductance than in eutherians (*7, 8*); however, at least some smaller marsupials have the same conductance as eutherians (*1*). Figure 1A also indicates that marsupial metabolism is reduced below that of eutherians at all temperatures below thermoneutrality. This would be the case if the generalized marsupial followed "Newtonian cooling" [figure 1 in (*9*)] with a body temperature below that of eutherians and a thermal conduc-

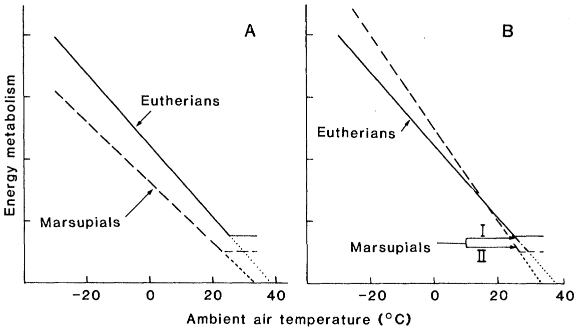

Fig. 1. Models of the relation of energy metabolism (H_m) to ambient air temperature (T_a) in marsupials and eutherians (A) from Dawson (*3*) and (B) proposed herein. The models (*7*) show a range of T_a's across which H_m is minimal and does not vary (horizontal lines). This T_a range is the zone of thermoneutrality and the H_m is often referred to as basal metabolism. At T_a's below thermoneutrality, metabolism follows the relationship $H_m = h(T_b - T_a)$ (*15*). For an animal following Newtonian cooling (*9*), the line relating H_m to T_a below thermoneutrality will project to a T_a equal to body temperature (T_b) when metabolism is zero. (B) Marsupials are shown to have a lower basal metabolism (dashed horizontal line) than eutherians in both I and II. In I, T_b and thermal conductance of marsupials are proposed to be similar to eutherians: they would then both follow the solid line below thermoneutrality. Alternatively, in II, marsupials are proposed to have a lower T_b but higher thermal conductance: marsupials would fall on the dashed line below thermoneutrality.

tance equal to or less than that of the eutherians.

A reduced metabolism below thermoneutrality for marsupials was at one time a reasonable prediction. Now enough data are available to evaluate this prediction by comparing direct measurements of metabolic rates of marsupials and eutherians of varying body mass at air temperatures below thermoneutrality.

We have done this analysis using oxygen consumption as a measurement of metabolism for both Australian and New World marsupials (*10*) and using established eutherian equations at both 10° and 20°C. We find (Fig. 2) that (i) the effect of body mass (the slope) is similar in both groups, but (ii) at the same body mass the marsupials have an equivalent or higher metabolism. The equations for the marsupials at 10° and 20°C (Fig. 2) have similar slopes but 10°C is significantly elevated above 20°C by approximately 65 percent (*11*). Although McNab suggested (*12*) that differences exist within the marsupials (and eutherians) that are based on food habits or habitat, we found no significant differences within the marsupials by comparing either carnivorous-insectivorous versus the others or forest versus nonforest dwellers. Equations at 10° and 20°C for arctic eutherians do not appear greatly different from the marsupials [figure 2 in (*13*)]. Oxygen consumption values predicted for marsupials are 46 percent higher at 10°C and 11 percent lower at 20°C than those predicted for arctic eutherians. We also have obtained allometric equations for 13 species of heteromyid rodent eutherians at 10° and 20°C (*14*). Equations for a generalized eutherian can be estimated from body temperature and the allometric relation for thermal conductance (*15*). These equations have similar slopes to those for marsupials; however, the equations for marsupials are elevated by approximately 30 percent over both the heteromyids and generalized eutherian.

These analyses lead us to propose alternative models (Fig. 1B) to that of Dawson. One possibility is that the relation between metabolism and air temperature for marsupials is identical to that of eutherians except for a reduction in basal metabolism (I in Fig. 1B). This model would suggest no differences in body temperature or thermal conductance, and this agrees with the data on the carnivorous dasyurids (*1*). Furthermore, we know of no investigation in which rigorous statistical treatment has been used to show differences between the two taxa for these variables. A second possibility is that the marsupials have a reduced basal metabolic rate, with slightly lower body temperatures but higher thermal conductances (II in Fig. 1B). This model is supported by the comparison with arctic eutherians in which marsupials have greater metabolism at 10°, but lower at 20°C. However, this model predicts a greater thermal conductance in marsupials, which does not seem to be the case (*1, 3*). Another model that could be proposed is that the marsupials do not follow Newtonian cooling; however, the majority of marsupials exhibit this characteristic (*16*).

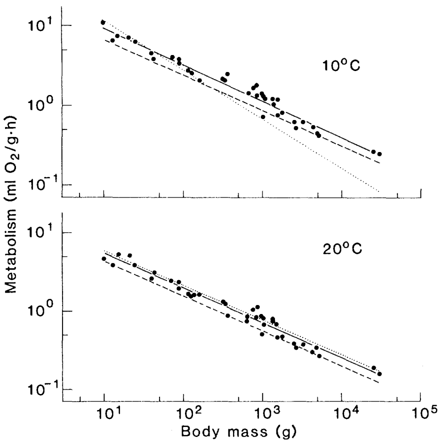

Fig. 2. The relation between oxygen consumption and body mass at 10°C and 20°C; data points are mean values for each species. The allometric equations describing the solid lines for the 33 species of marsupials (*10*) are: at 10°C, $y = 26.343\ g^{-0.457}$ ($n = 37$, $s_{yx} = 0.080$, $s_b = 0.15$, $s_a = 0.042$, $r^2 = 0.964$) and at 20°C, $y = 15.545\ g^{-0.450}$ ($n = 39$, $s_{yx} = 0.077$, $s_b = 0.014$, $s_a = 0.040$, $r^2 = 0.964$); equations for the dashed lines for the 13 species of heteromyids (*14*) are: at 10°C, $y = 19.525\ g^{-0.454}$ ($n = 111$, $s_{yx} = 0.083$, $s_b = 0.023$, $s_a = 0.022$, $r^2 = 0.784$) and at 20°C, $y = 12.764\ g^{-0.449}$ ($n = 111$, $s_{yx} = 0.095$, $s_b = 0.026$, $s_a = 0.021$, $r^2 = 0.734$); and equations for the dotted lines for the arctic mammals are given in (*13*). Species, body mass in grams and source if other than the present study are: *Antechinus maculatus*, 10; *Sminthopsis crassicaudata*, 14; *Antechinus stuartii*, 21; *Antechinomys spenceri*, 24; *Pseudantechinus macdonnellensis*, 42; *Dasycercus crisiticauda*, 88; *Dasyuroides byrnei*, 89; *Phascogale tapoatafa*, 160; *Satanellus hallucatus*, 131 and 638; *Dasyurus geoffroii*, 1,354 (*17*); *Dasyurops maculatus*, 1,782 (*1*); *Sarcophilus harrisii*, 5,050 (*1*); *Marmosa microtarsus*, 13 (*18*); *Monodelphis brevicaudata*, 40 and 111 (*12*); *Marmosa robinsoni*, 122 (*12*); *Caluromys derbianus*, 305 and 357 (*12*); *Metachirus nudicaudatus*, 336 (*12*); *Philander opossum*, 751 (*12*); *Lutreolina crassicaudata*, 812 (*12*); *Chironectes minimus*, 946 (*12*); *Didelphis marsupialis*, 1,000 and 1,329 (*12*); *Didelphis virginiana*, 1,548 and 3,257 (*12*); *Perameles nasuta*, 645 (*19*); *Macrotis lagotis*, 1,011 (*19*); *Isoodon macrourus*, 1,551 (*19*); *Cercartetus nanus*, 70 (*20*); *Phalanger maculatus*, 4,250 (*21*); *Pseudocheirus occidentalis*, 828 (*22*); *Potorous tridactylus*, 990 (*23*); *Setonix brachyurus*, 2,510 (*22*); *Lagorchestes conspicillatus*, 2,660 (*24*); *Macropus eugenii*, 4,960 (*25*); *Megaleia rufa*, 25,000 (*26*); *Macropus robustus*, 30,000 (*26*).

Regardless of which of the two models proposed here is correct, both indicate equal, if not higher, rates of metabolism at low temperatures for marsupials in comparison with eutherians. This is unexpected because of the reduction in metabolism in thermoneutrality in marsupials. The advantages of a reduced basal metabolism have been discussed at length (*14*). The advantage of an increase in basal metabolism has not been extensively addressed, but it has been considered disadvantageous since it raises the cost of living (*7*). McNab (*12*) suggested increased metabolism could be advantageous in shortening the gestation period but considers that explanation still inadequate. We have thought an advantage could be related to metabolic scope in that an increase in basal metabolism allows for an equivalent increase in maximum metabolism. For example, maximum metabolism for treadmill locomotion is approximately 26 percent lower in dasyurid marsupials than in eutherians; this difference is similar to the difference in basal rates (*5*). However, data indicate that in response to cold, small dasyurid marsupials have greater proportional metabolic scope than do eutherians (*4*). Finally, the differences in basal metabolism could be merely a phylogenetic coincidence. In any case, these data highlight the remarkable similarities, rather than the difference, in energetic performance of the two groups.

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11. Regression equations were calculated by the method of least squares after logarithmic transformations. Equations presented have slopes significantly different from zero (*F* test); the acceptable level of significance used throughout is $P < 0.05$. Differences between slopes and elevations were tested by analysis of covariance [G. W. Snedecor, *Statistical Methods* (Iowa State College, Ames, 1957), pp. 393–412]. Elevation of regression lines was compared only if the slopes were not significantly different; all differences in elevation between lines are presented at 450 g, which is the approximate mean body mass of the marsupial data.
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14. D. S. Hinds and R. E. MacMillen, in preparation. Allometric equations were obtained for heteromyid rodents at 5° and 15°C and were estimated at 10° and 20°C to compare with the marsupials; the prediction technique used is that described for 0°C by Hinds and MacMillen. To determine its accuracy we followed the same procedure at 5° and 15°C and compared these equations to those obtained when oxygen consumption was actually measured. The relation obtained from measured values had similar slopes to those obtained from predicted values; however, the latter equations are significantly elevated by 10 percent. Thus, the heteromyid equations (Fig. 2) have a greater elevation than if oxygen consumption had actually been measured.
15. For a generalized eutherian, the relation between oxygen consumption and mass below thermoneutrality can be derived from $H_m = h(T_b - T_a)$ where H_m is energy metabolism, h is thermal conductance, T_b is body temperature, and T_a is air temperature. At a T_a of 10°C, a T_b of 37°C, and h is related to body mass [C. F. Herreid and B. Kessel, *Comp. Biochem. Physiol.* **6A**, 57 (1962)] an estimate of this relation is: milliliters of oxygen per gram of body mass per hour = 27.81 $g^{-0.51}$ with g being body mass in grams.
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The Ultraviolet Receptor of Bird Retinas

Abstract. *The eyes of 15 species of birds from 10 families have some cones maximally sensitive at 370 nanometers in the near-ultraviolet. Spectral sensitivity was measured by recording extracellularly in opened eyecups, and a maximum in the ultraviolet was revealed by selectively adapting the retina with yellow background lights. The 370-nanometer spectral sensitivity function is attributed to receptors because its spectral position does not vary with the strength of adaptation and because it is present when the receptor potentials are isolated from the contributions of higher order retinal neurons by exposing the retina to sodium aspartate. These measurements demonstrate the basis for the ultraviolet sensitivity of birds that has been seen in behavioral experiments, and they provide further evidence that many vertebrates share with insects vision in the near-ultraviolet.*

Although it is widely believed that birds have color vision, in only a few species have demanding behavioral criteria been met, primarily in the pigeon (*1, 2*). Daws (*3*) and hummingbirds (*4, 5*) have also received critical attention.

In the retinas of birds (and some reptiles) each cone cell has a colored oil droplet at the distal end of the inner segment, so placed as to filter the light reaching the visual pigment. These droplets contain carotenoids with absorbances that can be greater than 20 (*6*). Because carotenoids absorb in the blue and violet regions of the spectrum, the traditional presumption has been that the vision of birds must be most effective at the long wavelength end of the visible spectrum. The functions of the cone oil droplets have been the subject of much speculation (*7*).

In recent years evidence has accumulated for multiple cone pigments in the retinas of pigeons and chickens. These new data lay to rest the idea that the cone oil droplets work together with a single cone visual pigment to produce several kinds of receptors with different spectral sensitivities. In chicken and pigeon direct evidence exists, from both retinal physiology (*8, 9*) and digitonin extraction (*10*), not only for several cone pigments, but for one with peak of absorption at 415 nm. Moreover, hummingbirds discriminate wavelengths as well in the violet as elsewhere in the visible spectrum (*5*). Still other behavioral evidence suggests that the visible spectrum of pigeons (*11*), hummingbirds (*12*), ducks (*13*), and a variety of passerines (*14*) extends into the near-ultraviolet (UV), but the basis for vision at such short wavelengths has not been demonstrated in birds.

We now report electrophysiological evidence that the retinas of hummingbirds and several species of passerines have cones with peak sensitivity in the UV at 370 nm. Birds were netted in southern Connecticut and dark-adapted overnight. They were anesthetized, their eyes were enucleated, and the front half of the eye was removed under dim red light. The back half of the eye was mounted in a moist chamber, and the eye was stimulated with light from a 150-W, optically stabilized xenon arc and a grating monochromator (*15*). Transretinal voltage responses were recorded with flat chlorided silver rings (*16*). Intensity of the stimulus was controlled with a pair of counterrotating optical wedges made of graded films of Inconel on quartz substrates. Stimuli consisted either of 100-msec flashes or a 25-Hz flicker, to which the rods respond poorly (*16*). In the latter case, the amplifier was also tuned to 25 Hz and had a noise level of about 0.2 μV. The stimuli were either presented in the dark or, to unmask the UV receptor, superimposed on a yellow background light (Schott sharp-cut filter, wavelengths longer than 530 nm), which was obtained from a 100-W tungsten-halogen lamp and combined with the stimulus beam by means of a dielectric beam splitter. Spectral sensitivity was determined by measuring the quantum flux required for a criterion response of 5 μV (single flashes) or 1 μV (25-Hz stimulus).

Figure 1A shows some results from the eye of a gray catbird (*Dumetella carolinensis*). Spectral sensitivity of the dark-adapted eye to single flashes peaked near 510 nm, and the response was dominated by rods. When the eye was stimulated with 25-Hz flicker, the spectral sensitivity peaked at about 580 nm and seemed to be due entirely to cones.

When the test lights were superim-