

Relating models of activity metabolism to the metabolic efficiency of steady swimming

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ABSTRACT

Power-law ($a + bU^c$) and exponential power-law (ae^{qU^c}) functional forms model activity metabolism (M_U) for fully submerged swimming animals, and are special cases of the power-law polynomial equation,

$$M_U = a(1 + a^{-1}bU^c)^\psi = \begin{cases} a + bU^c & \text{if } \psi = 1 \\ ae^{qU^c} & \text{if } \psi \rightarrow \infty \end{cases}$$

in which M_U is the observed total metabolic rate measured at an observed steady swimming speed, U . The relationship between the metabolic efficiency of steady swimming and the exponents of M_U is addressed in this paper to establish the use of c^{-1} (for $c > 1$) and ψ^{-1} (for $\psi > 1$) as optimal efficiencies for comparing the hydrodynamic and muscle metabolic efficiencies among fully submerged animals that engage in steady swimming activities. The metabolic efficiency of steady swimming is transformed into its ideal form ($\hat{\eta}_U$) from which the optimal hydrodynamic efficiency ($\hat{\eta}_h = c^{-1}$) and the optimal muscle metabolic efficiency ($\hat{\eta}_m = \psi^{-1}$) are derived. These optimal efficiencies are therefore ideal metabolic efficiencies measured at different optimal steady speeds. Subsequently, linear ($a + bU$) and exponential (ae^{qU}) models are approximations with divergent optimal muscle metabolic efficiencies ($\hat{\eta}_m \approx 1$ and $\hat{\eta}_m \ll 1$, respectively), but with a similar optimal hydrodynamic efficiency ($\hat{\eta}_h \approx 1$).

Keywords: Activity Metabolism; Exponent; Metabolic Efficiency; Power Law; Steady Swimming

1. INTRODUCTION

The activity metabolism (M_U) of a swimming animal

is the observed rate of total metabolic energy measured at an observed steady swimming speed, U . The functional forms that model M_U for a fully submerged animal are exponential (ae^{qU}) and power law ($a + bU^c$) [1-7]. Both forms, however, are special cases of the power-law polynomial equation [8],

$$M_U = a(1 + a^{-1}bU^c)^\psi = \begin{cases} a + bU^c & \text{if } \psi = 1 \\ ae^{qU^c} & \text{if } \psi \rightarrow \infty \end{cases} \quad (1)$$

in which the coefficients (a , b , c , and ψ) are hydrodynamical and physiological descriptors (see [7,8] for details). Note:

$$b = \psi^{-1}\beta \text{ and } q = a^{-1}\beta.$$

An important question that has not been addressed in the literature is how the swim-speed exponent (c) and the metabolic exponent (ψ) analytically relate to efficiencies. Experimental evidence suggests that c in $M_U|_{\psi=1}$ is a useful coefficient for comparing the swimming efficiency among different animals [9-14]. Papadopoulos [8] proposes that c in Equation (1) relates inversely to the propulsive (or hydrodynamic) efficiency of steady swimming and that ψ relates inversely to the metabolic conversion (or muscle metabolic) efficiency of steady swimming. But there is no analytical formulation that explicitly shows how c or ψ relates to efficiency. Although there is experimental evidence that suggests an inverse association between c and swimming efficiency, the definitive correspondence should be derived analytically from theory. And this also applies to the metabolic exponent, ψ .

This paper addresses the analytical relationship between the metabolic efficiency of steady swimming and the exponents of Equation (1). The analysis confirms that c^{-1} (for $c > 1$) is the optimal hydrodynamic efficiency of an animal in its ideal steady swimming state and that ψ^{-1} (for $\psi > 1$) is the optimal muscle metabolic efficiency of an animal in its ideal steady swimming state.

These optimal efficiencies can be used to compare the hydrodynamic and muscle metabolic efficiencies among fully submerged animals that engage in steady swimming activities. Furthermore, the optimal muscle metabolic efficiency (ψ^{-1}) determines the functional form of M_U .

2. RESULTS

The metabolic efficiency of steady swimming can be expressed as

$$\eta_U = \frac{P_U}{M_U} \tag{2}$$

where P_U is the rate of useful metabolic energy required to swim at U , and M_U is the rate of total metabolic energy generated by swimming at U . For convenience, let P_U be the rate of useful energy required to overcome the hydrodynamic drag. Then P_U is the drag power, which is proportional to the product of the power coefficient (C_p) and U cubed:

$$P_U \propto C_p U^3$$

where C_p for fully submerged animals that engage in either sustained steady swimming or burst steady swimming has been experimentally confirmed to be a power law with respect to the Reynolds number (Re) [15-17]:

$$C_p = \alpha \text{Re}^k \tag{3}$$

Since Re is proportional to U ,

$$\text{Re} \propto U$$

and that P_U is a constituent of M_U , the drag power (P_U) has the following identity (see [7], Appendix 1):

$$P_U = bU^c. \tag{4}$$

In addition to the experimental confirmation of Equation (3), power laws conform to standard hydrodynamic laws in which the logarithm of P_U and the logarithm of U are linearly related [7,12,15,16]:

$$\log P_U = \log b + c \log U$$

By substituting Equations (1) and (4) into Equation (2), η_U then has a stationary value (or a maximum) measured at a particular steady speed (see **Figure 1**): as U increases from $\eta_0 = 0$, η_U increases and then reaches its maximum, after which η_U decreases asymptotically towards zero (**Figure 1**). The steady speed, at which η_U is maximized, can be determined by η'_U (differentiating Equation (2) with respect to U), $\eta'_U = 0$ (equating η'_U to zero), and then solving for U :

$$U_{mc} = \left(\frac{a}{b(\psi - 1)} \right)^{1/c}, \begin{cases} a > 0 \\ b > 0. \\ \psi > 1 \end{cases} \tag{5}$$

Equation (5), which is an optimal U , is also the steady speed at which the metabolic cost of conversion

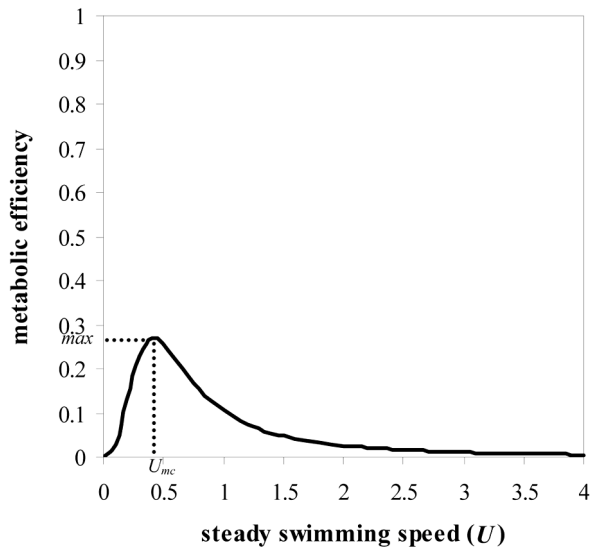


Figure 1. An example of the actual metabolic efficiency (Equation (2)) plotted with respect to the steady swimming speed (U). The values of the coefficients used to construct this example are as follows: $a = 0.05$, $b = 0.5$, $c = 2.5$, and $\psi = 1.9$. Note that η_U initially increases with increasing U and then reaches a maximum at U_{mc} , after which η_U decreases asymptotically towards zero.

(H_U),

$$H_U \equiv \eta_U^{-1} = \frac{M_U}{P_U}$$

is minimized. Swimming at U_{mc} thus optimizes the metabolic efficiency of the muscles used for steady swimming.

Substituting U_{mc} for U in Equation (2) yields the maximum metabolic efficiency of steady swimming:

$$\eta_m = \frac{bU_{mc}^c}{a(1 + a^{-1}bU_{mc}^c)^\psi} = \left(\frac{1}{\psi - 1} \right) \left(\frac{\psi - 1}{\psi} \right)^\psi. \tag{6}$$

Note that Equation (6) is exclusively dependent on the metabolic exponent, ψ : as ψ increases, η_m decreases. This equation, however, is not applicable for comparing the optimal muscle metabolic efficiency among different animals due to the fact that the equation is not a homogenous function of ψ : comparing any two different values of η_m , in which ψ can vary only with respect to different animals, is not evenly weighted. Let ψ_1 and $\psi_2 = \lambda\psi_1$ be two different values of ψ for two different animals. Then $\eta_m(\psi_1)$ and $\eta_m(\psi_2)$ are evenly comparable if $\eta_m(\psi_1) = \phi \cdot \eta_m(\lambda\psi_1)$ such that the weight, ϕ , is equivalent to the coefficient, λ . And that is not the case with Equation (6). Subsequently, homogenizing η_m would ensure that any two of its different values is evenly comparable, which would be applicable for comparing the optimal muscle metabolic efficiency among

different animals. This can be accomplished by transforming Equation (1) such that only one functional form is associated with metabolic efficiency. By raising the left-hand and right-hand side of Equation (1) to the ψ^{-1} power and multiplying that result by a^γ (in which $\gamma = 1 - \psi^{-1}$), the solution becomes

$$\hat{M}_U \equiv a^\gamma M_U^{1-\gamma} = a + P_U. \tag{7}$$

Equation (7) is an important variable: \hat{M}_U is the *ideal* total metabolic rate because it is the sum of a (the standard metabolic rate) and P_U , where a ($=\hat{M}_0$) describes the minimum metabolic rate required to sustain physiological maintenance [2,3], while $P_U = (bU^c)$ describes the rate of useful metabolic energy required to overcome the hydrodynamic drag. Since Equation (5) must be satisfied, the inequality,

$$\hat{M}_U < M_U$$

implies that an *actual* animal could never achieve \hat{M}_U but only in its *ideal* steady swimming state, that is, only as the limit of M_U as η_m approaches 1. By substituting \hat{M}_U for M_U in Equation (2), the ideal metabolic efficiency of steady swimming,

$$\hat{\eta}_U = \frac{P_U}{\hat{M}_U} \tag{8}$$

can thus be compared with η_U (see **Figure 2**). Notice that since \hat{M}_U (for any $\psi > 1$) is less than M_U , $\hat{\eta}_U$ must be greater than η_U (**Figure 2**).

Unlike Equation (2), Equation (8) is expressed as one functional form, the result of which yield homogeneous functions that are suitable for comparing the optimal efficiencies among different animals. In particular, substituting U_{mc} for U in Equation (8) yields

$$\hat{\eta}_m = \frac{bU_{mc}^c}{a + bU_{mc}^c} = \frac{1}{\psi}. \tag{9}$$

Equation (9) is the optimal muscle metabolic efficiency of an animal in its ideal steady swimming state (see **Figure 2**). Specifically, $\hat{\eta}_m$ is the ideal metabolic efficiency measured at the steady speed— U_{mc} —at which η_U is maximized (or H_U is minimized). As a result, $\hat{\eta}_m$ can be used to compare the optimal muscle metabolic efficiency among different animals that engage in steady swimming activities.

The next part to this analysis is to determine the optimal hydrodynamic efficiency of an animal in its ideal steady swimming state. The product of the hydrodynamic efficiency and muscle metabolic efficiency yields the overall (or energetic) efficiency of steady swimming [3,9]. An important variable that accounts for the energetic efficiency of steady swimming is the metabolic cost of transport (F_U) [18-20]:

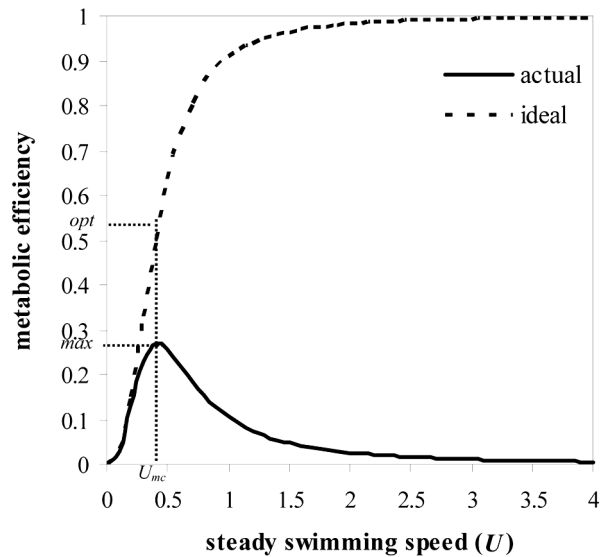


Figure 2. An example of the metabolic efficiency plotted with respect to the steady swimming speed (U). The solid line is the actual efficiency, η_U (= Equation (2)), whereas the dotted line is the ideal efficiency, $\hat{\eta}_U$ (= Equation (8)). The values of the coefficients used to construct this example are as follows: $a = 0.05$, $b = 0.5$, $c = 2.5$, and $\psi = 1.9$. The optimal metabolic efficiency of the muscles used for steady swimming is the ideal efficiency measured at U_{mc} . Note that $\hat{\eta}_U$ continually increases asymptotically towards 1.

$$F_U = \frac{M_U}{U}. \tag{10}$$

Equation (10) describes the actual total metabolic energy generated per unit of distance traveled [18-20], and has, like H_U , a minimum measured at a particular U . By differentiating F_U with respect to U , equating F'_U to zero, and then solving for U , the steady speed that minimizes Equation (10) is (see [8])

$$U_{mt} = \left(\frac{a}{b(c\psi - 1)} \right)^{1/c}, \begin{cases} a > 0 \\ b > 0 \\ c\psi > 1 \end{cases}. \tag{11}$$

Equation (11), like Equation (5), is an optimal U . Thus, swimming at U_{mt} optimizes the energetic efficiency of steady swimming. It should be noted that Equation (11) is traditionally derived by equating $F'_U|_{\psi=1}$ to

zero and then solving for U (see [21]), though ψ is, in fact, a coefficient and thus should not be constrained to any value [8]. Also, Weihs' [22] optimal cruising speed, in which C_p is assumed not to vary with Re (or $c\psi = c = 3$), is a special case of Equation (11). Such simplifying assumptions are not relevant to this paper. Substituting U_{mt} for U in Equation (8) yields

$$\hat{\eta}_* = \frac{bU_{mt}^c}{a + bU_{mt}^c} = \frac{1}{c\psi} \tag{12}$$

Equation (12) is the optimal energetic efficiency of an animal in its ideal steady swimming state. Specifically, $\hat{\eta}_*$ is the ideal metabolic efficiency measured at the steady speed— U_{mt} —at which F_U is minimized. Therefore, $\hat{\eta}_*$ can be used to compare the optimal energetic efficiency among different animals that engage in steady swimming activities. Since the product of the hydrodynamic efficiency and muscle metabolic efficiency yields the energetic efficiency of steady swimming (see [3,9]), the optimal hydrodynamic efficiency ($\hat{\eta}_h$) of an animal in its ideal steady swimming state can thus be determined by the ratio of $\hat{\eta}_*$ to $\hat{\eta}_m$:

$$\hat{\eta}_h = \frac{\hat{\eta}_*}{\hat{\eta}_m} = \frac{1}{c}$$

where c is the swim-speed exponent. Alternatively, $\hat{\eta}_h$ can be derived by differentiating the ideal cost of transport (\hat{F}_U),

$$\hat{F}_U = \frac{\hat{M}_U}{U}$$

with respect to U , equating \hat{F}'_U to zero, solving for U ,

$$\hat{U}_{mt} = \left(\frac{a}{b(c-1)} \right)^{1/c}, \begin{cases} a > 0 \\ b > 0 \\ c > 1 \end{cases} \quad (13)$$

and then substituting \hat{U}_{mt} for U in Equation (8):

$$\hat{\eta}_h = \frac{b\hat{U}_{mt}^c}{a + b\hat{U}_{mt}^c} = \frac{1}{c} \quad (14)$$

As a result, Equation (14) is the ideal metabolic efficiency measured at the steady speed— \hat{U}_{mt} —at which \hat{F}_U is minimized, and can thus be used to compare the optimal hydrodynamic efficiency among different animals that engage in steady swimming activities.

3. DISCUSSION

Steady swimming is observed in animals engaging in ecologically important activities such as competing for limited resources, seeking favorable abiotic conditions, and migration [23-27]. During such activities, an animal swims at an optimal steady speed to minimize its metabolic cost. For example, during migration, an animal maximizes its distance per unit of total metabolic energy by swimming at the steady speed (U_{mt}) at which the metabolic cost of transport (F_U) is minimized [22,28]. Thus maximizing the distance per unit of total metabolic energy is essential for optimizing the steady swimming performance during migration. Equally essential, however, is optimizing the steady swimming performance during activities in which maximizing distance is not essential. For example, while competing for limited re-

sources within a microhabitat, an animal maximizes its useful metabolic energy per unit of total metabolic energy by swimming at the steady speed (U_{mc}) at which the metabolic cost of conversion (H_U) is minimized. Hence, an animal can optimize its steady swimming performance for different activities by swimming at U_{mt} (the steady speed at which F_U is minimized) or U_{mc} (the steady speed at which H_U is minimized). But there is a fundamental difference between these two objectives: H_U , unlike F_U , is dimensionless; the inverse of H_U is, in fact, the metabolic efficiency of steady swimming, η_U (= Equation (2)); see **Figure 1**. A transformation of η_U is then formulated in order to yield optimal efficiencies that are homogenous functions of c and ψ of different animals. This is particularly important when comparing the optimal efficiencies among different animals. This transformation (see Equation (7)) yields the ideal metabolic efficiency of steady swimming, $\hat{\eta}_U$ (= Equation (8)); see **Figure 2**, for which ψ can be any value greater than 1. The ideal steady swimming state of an animal can thus be interpreted as a special case of Equation (2) in which the maximum metabolic efficiency, η_m (= Equation (6)), approaches 1.

Substituting U_{mt} (which is the steady speed that optimizes the energetic efficiency of steady swimming) for U in $\hat{\eta}_U$ yields the optimal energetic efficiency of an animal in its ideal steady swimming state and is identical with Equation (12):

$$\hat{\eta}_* = \frac{1}{c\psi}, c\psi > 1,$$

where c and ψ are the exponents in Equation (1), which describes the activity metabolism (M_U) of a fully submerged animal engaged in steady swimming. The steady speed that optimizes the metabolic efficiency of the muscles used for steady swimming— U_{mc} —is then substituted for U in $\hat{\eta}_U$ to yield the optimal muscle metabolic efficiency of an animal in its ideal steady swimming state (see **Figure 2**),

$$\hat{\eta}_m = \frac{1}{\psi}, \psi > 1,$$

which is identical with Equation (9). Since the energetic efficiency is the product of the hydrodynamic and muscle metabolic efficiencies [3,9], the optimal hydrodynamic efficiency ($\hat{\eta}_h$) is simply the ratio of $\hat{\eta}_*$ to $\hat{\eta}_m$:

$$\hat{\eta}_h \equiv \frac{\hat{\eta}_*}{\hat{\eta}_m} = \frac{1}{c}, c > 1,$$

which can also be derived by substituting into $\hat{\eta}_U$ the steady speed (\hat{U}_{mt}) that optimizes the hydrodynamic efficiency of an animal in its ideal steady swimming state (see Equations (13) and (14)). The optimal efficiencies, $\hat{\eta}_h$ and $\hat{\eta}_m$, can thus be used to compare the hydrody-

dynamic and muscle metabolic efficiencies among fully submerged animals that engage in steady swimming activities. Furthermore, the fact that c and ψ are independent of the scale of M_U and U further validates the use of $\hat{\eta}_h$ and $\hat{\eta}_m$ as ideal efficiencies for comparing the optimal hydrodynamic and optimal muscle metabolic efficiencies among different animals.

It is important to note that neither c nor ψ can equal exactly 1; otherwise, $\hat{\eta}_h$ or $\hat{\eta}_m$ is undefined (see Equations (5) and (13)). As a result, the first-degree power-law functional form of M_U can be only approximated:

$$M_U \approx a + bU^c \text{ when } \hat{\eta}_m \approx 1$$

Also, since the value of ψ is estimated by fitting Equation (1) to activity metabolism, ψ cannot approach infinity, because infinity is not a number. The curve-fit estimate of ψ , however, can be a value much greater than 1. And so, the exponential power-law functional form of M_U can be only approximated [8]:

$$M_U \approx ae^{qU^c} \text{ when } \hat{\eta}_m \ll 1$$

Notice that the functional form of M_U (= Equation (1)) depends on the value of $\hat{\eta}_m$; this implies that the power-law ($a + bU^c$) and exponential power-law (ae^{qU^c}) models suggest different biology with regard to the metabolic conversion (or muscle metabolic) efficiency of steady swimming: a very high value of $\hat{\eta}_m$ (i.e., when $\hat{\eta}_m \approx 1$) implies that the activity metabolism of an animal is best modeled as a first-degree power-law polynomial, whereas a very low value of $\hat{\eta}_m$ (i.e., when $\hat{\eta}_m \ll 1$) implies that the activity metabolism of an animal is best modeled as an exponential power law. Of course, the linear form,

$$M_U \approx a + bU \text{ when } \hat{\eta}_h \approx 1 \text{ and } \hat{\eta}_m \approx 1$$

which is a special case of $a + bU^c$, is approximated when $\hat{\eta}_h$ and $\hat{\eta}_m$ are both very high values. And the exponential form,

$$M_U \approx ae^{qU} \text{ when } \hat{\eta}_h \approx 1 \text{ and } \hat{\eta}_m \ll 1$$

which is a special case of ae^{qU^c} , is approximated when $\hat{\eta}_h$ is a very high value and $\hat{\eta}_m$ is a very low value. In essence, the linear form of M_U suggests high hydrodynamic and high muscle metabolic efficiencies because it has no or little curvature with respect to U . The exponential form of M_U , however, suggests that the two efficiencies are compensatory: hydrodynamic efficiency is very high, while muscle metabolic efficiency is very low; a high hydrodynamic efficiency thus compensates for a low muscle metabolic efficiency.

The metabolic efficiency of steady swimming (Equation (2)) has an intimate connection with activity metabolism. To understand why this is so, consider the fol-

lowing equivalence of \hat{M}_U :

$$\exp\left(\int \frac{\hat{\eta}_U}{\hat{\eta}_h U} dU\right) = e^{C_1} \hat{M}_U = \hat{M}_U, \quad (15)$$

where $C_1 = \ln(1) = 0$ is the constant of integration, which is determined by satisfying the condition $\hat{M}_0 = a$. The left-hand side of Equation (15) is exclusively in terms of efficiency ($\hat{\eta}_U$) and speed (U)—two basic terms in hydrodynamics. Moreover, as Papadopoulos [8] noted, Equation (1) can be derived from Equation (15) simply by multiplying $\hat{\eta}_m$ (the optimal muscle metabolic efficiency) by $\hat{\eta}_h$ (the optimal hydrodynamic efficiency) or replacing $\hat{\eta}_h$ with $\hat{\eta}_* = \hat{\eta}_h \hat{\eta}_m$ (the optimal energetic efficiency):

$$\exp\left(\int \frac{\hat{\eta}_U}{\hat{\eta}_* U} dU\right) = e^{C_2} \hat{M}_U^\psi = M_U, \quad (16)$$

where the constant of integration, $C_2 = \ln(a^{1-\psi})$, is determined by satisfying the condition $M_0 = a$. Thus, Equation (16) is identical with Equation (1):

$$M_U = a^{1-\psi} \hat{M}_U^\psi = a(1 + a^{-1}bU^c)^\psi$$

Equations (15) and (16) show analytically the unique relationship between activity metabolism and the metabolic efficiency of steady swimming. And so, with regard to efficiency, the difference between the ideal total metabolic rate (= Equation (7)) and the actual total metabolic rate (= Equation (1)) is the optimal muscle metabolic efficiency, $\hat{\eta}_m$; this coefficient is clearly important to consider not only because it takes into account muscle metabolic efficiency, but also because it determines the functional form of M_U [8].

4. CONCLUSIONS

A fully submerged animal that engages in steady swimming has an ideal metabolic efficiency ($\hat{\eta}_U$) from which the optimal efficiencies, $\hat{\eta}_h$ and $\hat{\eta}_m$, are derived (Equations (1)-(14)). The optimal hydrodynamic efficiency ($\hat{\eta}_h$) and the optimal muscle metabolic efficiency ($\hat{\eta}_m$) are thus ideal metabolic efficiencies measured at the optimal steady speeds, \hat{U}_{mt} and U_{mc} , respectively (see **Figure 2**). And from hydrodynamic principles (see [3,9]), the product of $\hat{\eta}_h$ and $\hat{\eta}_m$ represents the optimal overall (or optimal energetic) efficiency ($\hat{\eta}_*$) of an animal in its ideal steady swimming state:

$$\hat{\eta}_* = \hat{\eta}_h \hat{\eta}_m = c^{-1} \psi^{-1}.$$

Although the coefficients $\hat{\eta}_h = c^{-1}$ and $\hat{\eta}_m = \psi^{-1}$ are inverses of the exponents in Equation (1) and thus remain constant with respect to U for any animal, they can indeed vary only with respect to different animals. Comparing $\hat{\eta}_h$ and $\hat{\eta}_m$ among different animals requires

that these optimal efficiencies are homogenous functions of c and ψ : $\hat{\eta}_h$ and $\hat{\eta}_m$ are, in fact, homogenous due to the transformation of Equation (2) into Equation (8), which is the ideal form of η_U . Furthermore, since $\hat{\eta}_h$ and $\hat{\eta}_m$ are inverses of the exponents in Equation (1), the different models of M_U exclusively arise from the different values of $\hat{\eta}_h$ and $\hat{\eta}_m$.

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