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## On the Time Allometry of Co-ordinated Rhythmic Movements

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The focus is the power formulae relating periodic time in terrestrial locomotion and flight to mass and length. The periodic timing of limbs and wings oscillating comfortably in absolute co-ordination is viewed as the characteristic period  $\tau_0$  of a system in which the free, undamped oscillatory motion of a point mass  $m$  at a distance  $l$  from a fixed axis does work against two conservative forces. These forces are in the form of gravity  $g$  acting on the point mass and a spring of stiffness  $k$  acting at a distance  $b$  from the axis. The system's characteristic period can be expressed most simply as:  $\tau_0 = 2\pi[m^2/(mgl + kb^2)]^{1/2}$ . In the biological instantiation of this hybrid mass-spring/simple pendulum system, muscular and other tissues function as the spring that elastically stores and releases mechanical energy. Regular oscillations are brought about and sustained by a muscular driving force that ordinarily is close to resonance. The resultant dynamical regime—basically, raising and lowering a mass at regular intervals with respect to gravity—is referred to as the pendular clocking mode of movement organization. The mode is investigated in the laboratory by having a person swing pendulums in the left and right hands comfortably at a common period and a fixed phase. In absolute co-ordination, two wrist-pendulum systems can be interpreted physically as a virtual single system. The evidence suggests that the scalings of the periodic times of such systems to mass and to length follow directly from the dynamical properties inherent in the resonance equation of the pendular clocking mode. Recourse to biological constants to rationalize the time scale is unnecessary. Experiments on human wrist-pendular activity and detailed analyses of the mass and length dependencies of the locomotory cycle times of quadrupeds, large birds, small passerines, hummingbirds, and insects are performed with respect to the dynamical properties predicted for systems in the pendular clocking mode. The major conclusion is that all the time scales of terrestrial and aerial locomotion are the consequences of a single dynamical regime. Differences in locomotory time allometries follow systematically from differences in the length scale and differences in the relation of mass to length.

Evidence has accumulated through allometry (the quantitative analysis of body size relations) that physiological, developmental and ecological cycle times exhibit nearly

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parallel exponential relations to body size as indexed by body mass or by a representative linear dimension (e.g. Lindstedt & Calder, 1981). The cycle times in question span 10 orders of magnitude, from milliseconds to decades of years. The concept of an invariant physiological time scale, introduced by Adolph (1949) and Hill (1950), was elevated by Stahl (1962) to a fundamental design principle for living systems, viz., synchronicity of times.

"In the analysis of growth and related matters it has become clear that two principles play a key role in biological analysis: conservation of volume and synchronism of times. . . . Corresponding processes are expected to occur in corresponding times. It appears that the time scale is uniformly that of  $M^{0.25}$  to  $M^{0.30}$  in mammals and probably in many other organisms (p. 209)."

The proposed fundamental physiological time scale—expressed in terms of body mass and designated by  $M$  in the preceding—shows up in various rhythmic activities (see Calder, 1984). Observations made over many animals differing markedly in size reveal that the cycle times of heartbeat, breathing and peristaltic "gut beat" all scale in the body mass<sup>1/4</sup> to body mass<sup>1/3</sup> range. The more relevant observations for our present purposes are those on locomotion. As we detail below, wing cycle times of insects scale in the body mass<sup>1/4</sup> range. In contrast, the step cycle times of the three major quadruped gaits all scale in the body mass<sup>1/8</sup> to body mass<sup>1/6</sup> range as do the wing cycle times of large birds. These latter scalings, however, can be interpreted as manifestations of the same fundamental, physiological time scale that governs heartbeat, breathing and peristalsis; it is merely that the geometric setting for the fundamental time scale is different (Calder, 1984; McMahon, 1975, 1980). When humans move masses comfortably in pendular fashion their steady-state rhythms scale as mass<sup>1/16</sup>, where the mass is the rhythmically moved mass (Kugler & Turvey, 1987). This allometry can also be interpreted as the fundamental time scale manifest within a particular geometric setting.

In this paper the hypothesis of a single time allometry for locomotory rhythms, grounded in constants of biological tissue (as might be suggested by the theories of Economos, 1982; Gunther & Morgado, 1982; Platt & Silvert, 1981), is rejected in favor of the hypothesis of multiple time allometries (a) all based in a single dynamical regime, (b) dependent on the length scale, and (c) dependent on the relation of mass to length. Expressed most simply, the dynamical regime is the regular, periodic displacement of a point mass about a fixed axis of rotation relative to two conservative forces, namely, gravity and an elastic force. (In terms of this simple expression, a mass to length scaling means that the point mass's distance from the axis of rotation is proportional to the point mass.) By definition, the work done in overcoming the two conservative forces during periodic displacement is recoverable and stored as potential energy. In biological instances of this regime, the regular periodic displacement is achieved and sustained by contractile, muscular forces; and the elastic potential force is provided by the animal's tissues, primarily muscular and tendonous tissues, and adjustable—within limits and depending on species—by neural processes. Kugler & Turvey (1987) have referred to this regime as the "pendular, clocking mode" of movement organization: a mass is raised and lowered with respect to gravity at regular intervals.

To examine the pendular, clocking behavior of a single limb, a weighted pendulum is held in one hand and made to oscillate by rhythmic movements of the wrist joint. The person is instructed to swing at the most comfortable tempo. This instruction is intended to encourage minimal muscular energy and a rhythmic movement at or close to the characteristic or resonance period (see below). For different weighted pendulums (different shaft lengths, different added masses) the person settles at different tempos. To examine the pendular, clocking behavior of the two limbs, a person holds two pendulums, one in each hand, and swings both simultaneously at the wrists. The two pendulums can be swung in phase (0 degrees difference) or out of phase (180 degrees difference), resembling the organization of symmetric and asymmetric gaits, respectively (e.g. Grillner, 1975). Whatever the phase relation the person is instructed to swing both pendulums at the same tempo, and to do so comfortably. For different pairs of weighted pendulums the person settles at different, common tempos.

A single wrist-pendulum system, when looked at just in terms of the material distribution relative to the point of rotation, is a compound pendulum. There are three masses rotating about a point in the wrist joint, namely, the mass of the pendulum shaft or rod, the mass of the added weights and the mass of the hand. The distances of the centers of these masses from the common point of rotation are not equal. Nevertheless, the total mass of a wrist-pendulum system can be characterized as concentrated at a single distance from the point of rotation. This is achieved by computing the moment of inertia of the system by idealizations of the mass shapes and by applications of the parallel axis theorem (Hartog, 1948) and then calculating the simple pendulum equivalent of the compound pendulum in the ordinary manner (see Kugler & Turvey, 1987; Turvey *et al.*, 1986). The resultant characterization identifies a single mass quantity and a single length quantity of a wrist-pendulum system. This characterization can be extended to two coupled wrist-pendulum systems. Even though they are connected neurally rather than connected rigidly they can be treated as if they are connected rigidly. That is, in combination, a right wrist-pendulum system and a left wrist-pendulum system can be conceptualized as a compound pendulum. As a result, the total mass of two wrist-pendulum systems, coupled to oscillate at the same tempo—that is, in absolute co-ordination (von Holst, 1939/1973)—can be characterized as a single point mass at a distance from a single “virtual” point of rotation (see Kugler & Turvey, 1987, or Turvey *et al.*, 1986, for details). We refer to systems characterized in the foregoing manner as virtual single systems.

### Time Allometry of Wrist-Pendulum Systems

Kugler & Turvey (1987) derived a time allometry for (single and virtual single) wrist-pendulum systems, namely,

$$\tau_0 \propto m^{1/16} l^{1/2} \quad (1)$$

from two sources. One source was the so-called “basic empirical scaling relations” for biological systems, appropriately rationalized by a particular choice of universal

biological constants. The other source was the scaling relation defined by the dimensional composition of a wrist-pendulum system modeled mechanically as a hybrid mass-spring/simple pendulum system. Figure 1 presents the model. The pendulum consists of a stiff weightless rod of length  $l$  carrying a mass  $m$  on its end.

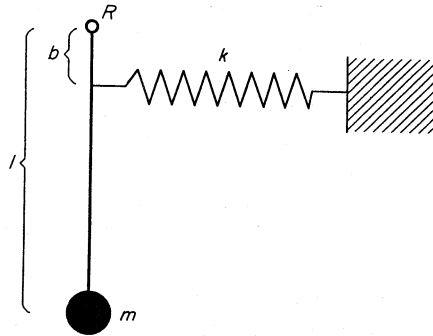


FIG. 1. The hybrid mass-spring/simple pendulum model.

At a distance  $b$  from the upper end is a spring attached to the rod. The spring represents the neuromuscular organization providing a restoring force per unit displacement of the mass. It is assumed that the spring constant  $k$  is (a) a macroscopic property assembled from both elastic and viscous components at a more microscopic level and (b) a unitary property defined over the radial and ulnar flexors. Ignoring amplitude, the equation for the characteristic or resonance period of the free, undamped system depicted in Fig. 1 is

$$\tau_0 = 2\pi [ml^2 / (mlg + kb^2)]^{1/2}. \quad (2)$$

A single scaling relation between  $\tau_0$ ,  $m$  and  $l$  cannot be derived from the preceding equation for characteristic period. To begin with, the summation sign prohibits an analytic solution. Second,  $m$  and  $l$  are uncorrelated so one quantity cannot be expressed in terms of the other. To converge on a single time scale an expression is required of the relation between  $\tau_0$  and  $m$  and  $l$  for circumstances in which  $m$  and  $l$  are the only independent variables; that is, an expression for how  $\tau_0$  would vary with variations in  $m$  and  $l$  if the context of restoring forces were constant and independent of  $m$  and  $l$ . The quantities in this expression must enter into products and quotients. (If they enter into additions and subtractions the requisite scaling relation cannot be determined.) And the expression must be dimensionally homogeneous. One relation among the quantities identified in Fig. 1 meets these requirements, namely

$$\tau_0 \propto (ml^2 / bgk)^{1/4}. \quad (3)$$

With respect to the right-hand side of this equation,  $g$  (the acceleration due to gravity),  $k$  (the stiffness of the spring) and  $b$  (the perpendicular distance from the spring's point of application to the axis of rotation) are all constants;  $m$  (the mass) and  $l$  (the length from the axis of rotation to the mass) are the sole variables. For

a system such as that depicted in Fig. 1, with uncorrelated mass and length, if the spring coefficient is invariable and if it is indifferent to  $m$  and  $l$ , then variations in periodic time  $\tau_0$  must go as  $(ml^2)^{1/4}$ , that is, as  $m^{1/4}l^{1/2}$ .

This scaling relation is defined for any system dimensionally identical to the system depicted in Fig. 1 and assembled with (quasi) independent mass and length magnitudes. The concern here, however, is with a biological instantiation of the depicted system. As noted above, a major empirical observation is that, for mammalian species, biological time scales as biological mass to approximately the 1/4 power (and as any representative biological length to approximately the 1 power). Economos (1982) has hypothesized that this fundamental time scale is grounded in three (muscle) tissue constants:

$$\text{constancy of density, } m = c_1 l d^2; \quad (4)$$

$$\text{constancy of elasticity, } l = c_2 d^{2/3}; \quad (5)$$

$$\text{constancy of tensile strength, } f = c_3 A = c_3' d^2, \quad (6)$$

where  $m$  is muscle mass,  $l$  is muscle length,  $d$  is muscle diameter,  $A$  is cross-sectional area (proportional to  $d^2$ ),  $f$  is force, and the  $c$ s are constants. From the constancies of density and elasticity, dimensional considerations yield the mass to length proportionality of  $m \propto l^4$ . From the constancies of density and tensile strength, dimensional considerations yield the time to length proportionality of  $t \propto l^1$  (see Economos, 1982, and Kugler & Turvey, 1987, for details). Combining the two preceding allometries yields  $t \propto m^{1/4}$ . If, as is being suggested, the tissue constants determine the fundamental length- and mass-based time scales, then it ought to be the case that a biological system brings these fundamental time scales into any timing task that it executes. On this assumption the relation identified by (3) can be "biologized" to produce the proportionality

$$\tau_0 \propto [(m^{1/4} l^2) / b g k]^{1/4}. \quad (7)$$

The key idea behind (7) is that, in assembling a wrist-pendulum system, a biological system (a person) for which  $\tau_0$  scales, in dimensional terms, as  $m^{1/4}$  and  $l^1$ , simulates a simple dynamical system for which  $\tau_0$  scales, in dimensional terms, as  $m^{1/4}$  and  $l^{1/2}$ . According to this idea, to obtain the proper scaling relation, the biological scaling requirements (the fundamental physiological time scales) of the simulator must be embedded in the mechanical scaling requirements of the system simulated. Hence, in dimensional terms, the periodic timings of wrist-pendulum systems for which variations in mass and length are uncorrelated scale as  $m^{1/16} l^{1/2}$  or  $m^{0.0625} l^{0.5}$ . Empirically, the scaling relation was found to be  $m^{0.056} l^{0.469}$ , with 95% confidence limits of 0.024 and 0.094 for mass and 0.429 and 0.540 for length, respectively (Kugler & Turvey, 1987).

In what follows we show that the time scale of wrist-pendular activity with uncorrelated mass and length is inherent in equation (2). No presuppositions about fundamental physiological time scales grounded in biological constants are required for its rationalization. The predicted and observed time scale is, more simply and more elegantly, a matter of the physics of the pendular clocking mode.

### The Equation of the Pendular Clocking Mode

This section explores the properties of equation (2), which will be referred to as the equation of the pendular clocking mode. Our goal in this section is to underscore the generality of this particular dynamical regime and to show how it gives rise to different time scales under different circumstances (different mass-to-length relations, different magnitudes of elastic energy at resonance).

#### EQUIPOTENTIAL LINES WITH UNCORRELATED MASS AND LENGTH

Forty-nine pairs of  $m$ ,  $l$  values were selected under the restriction of independence of  $m$  from  $l$ . Forty-two  $K$  values (where  $K = kb^2$ ) were selected ranging from  $-5.0$  to  $+20.0$ . For each  $K$  value—an equipotential line—the periods of the 49 systems defined by the 49  $m$ ,  $l$  pairings were computed using equation (2). The logarithms of these periods were then regressed simultaneously on the logarithms of the  $m$  and  $l$  values. Figure 2 shows the outcome. It plots the  $m$  and  $l$  exponents— $M$  exp and  $L$  exp, respectively—as a function of  $K$ . Inspection of the figure reveals that both exponents change systematically with  $K$ ; there are multiple time scales. Closer inspection reveals that in the range of  $K$  values close to zero,  $M$  exp approximates  $0.0625$  and  $L$  exp approximates  $0.5$ .

The equation of motion for the system depicted in Fig. 1 is:

$$ml^2(d^2\phi/dt) + mgl \sin \phi + kb^2 \sin \phi \cos \phi = 0. \quad (8)$$

To derive equation (2), it is assumed that the amplitude of oscillation ( $\phi$ ) is small and constrained to the range in which  $\sin \phi$  approximates  $\phi$ , and  $\cos \phi$  approximates one. Essentially, this assumption allows for the treatment of the system depicted in Fig. 1 as linear, permitting, thereby, the ready determination of a simple expression relating  $\tau_0$ , and  $K (= kb^2)$ .

Amplitudes in wrist-pendular behavior tend to be consonant with this assumption. Consequently, equation (2) was used to derive estimates of  $K$  for virtual single

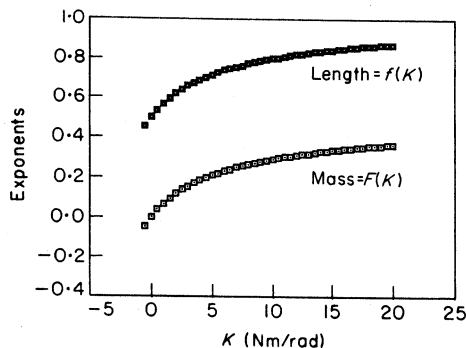


FIG. 2. For periodic times generated from equation (2) for various mass and length combinations, with mass and length uncorrelated, the scaling of period to mass ( $M$  exp) and length ( $L$  exp) is a function of the value of the elastic torsional stiffness ( $K$ ).

& Turvey's (1987) main experiment,  $K$  increased linearly with moment of inertia; for one subject a decreasing linear relation was observed. The lower and upper  $K$  values were  $-2.453$  Nm/rad and  $3.263$  Nm/rad, respectively. Figure 3 shows how the exponents behave inside this  $K$  range for periodic times generated through equation (2). A best fitting line is included in the figure to provide a simple basis for estimating  $M_{exp}$  and  $L_{exp}$  given  $K$ . Inspection suggests that, if in the formation of wrist-pendular clocking behavior  $K$  approximates 1 on the average, then the prediction from the pendular clocking mode equation for uncorrelated masses and lengths is that  $M_{exp}$  and  $L_{exp}$  will be in the vicinity of 0.06 and 0.54, respectively.

The preceding analysis suggests that the  $m^{1/16}l^{1/2}$  time allometry advanced by Kugler & Turvey (1987) is, in fact, only an approximation. There is a variable time scale (it varies with  $K$ ) rather than a fixed time scale. Moreover, and more importantly, the preceding analysis questions the strategy, detailed above, by which the  $m^{1/16}l^{1/2}$  time allometry was derived. In their derivation Kugler & Turvey (1987) assumed that the proposed fundamental physiological time scales of  $m^{1/4}$  and  $l^1$  are carried around, as it were, by biological systems (by virtue of tissue constants) to be inserted into, and rescaled by, particular biomechanical circumstances. It would now seem to be the case that the empirically observed  $m^{0.056}l^{0.469}$  time allometry for wrist-pendulum systems was a direct consequence of assembling the systems, for which amplitude values are unavailable. For three subjects in Kugler pendular clocking mode over (a) a restricted range of  $K$  values and (b) wrist-pendulum systems whose masses and lengths were uncorrelated. That is to say, the observed time allometry followed directly from the pendular clocking mode equation

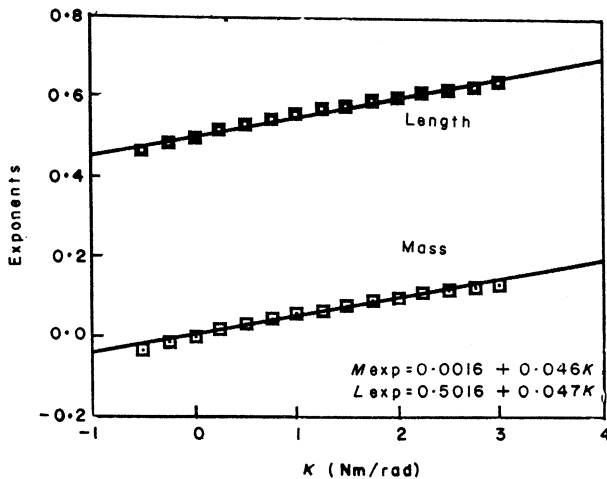


FIG. 3. Time scales as a function of  $K$  in the range of  $K$ s found in the main experiment of Kugler & Turvey (1987). If  $K$  is in the vicinity of 1, then the time scales generated by the pendular clocking mode equation are commensurate with those observed empirically.

confined in a particular fashion. The human subjects in the Kugler & Turvey experiments did not bring times scales into the task. Rather, the time scales they exhibited were defined intrinsically by the task—by the pendular clocking dynamical regime—and the circumstances under which it was performed.

THE  $K \times G$  SPACE AND TRAJECTORIES DEFINED BY CONSTANT  $K/G$

Ignoring amplitude, the two terms in the denominator of the pendular clocking mode equation are  $mlg$  and  $kb^2$ . These two terms identify two torsional stiffnesses (dimensionally,  $ML^2T^{-2}$ ) tied to two different spring constants. For convenience we will refer to  $mlg$  as  $G$  to correspond to the use of  $K$  for  $kb^2$ . Obviously when a periodic time is produced by the pendular clocking organization,  $G$  and  $K$  must stand in some particular relation to each other. Because of their common dimensionality it is always possible to express either one (say  $K$ ) in units of the other ( $G$ ).

Figure 4 represents the  $K \times G$  co-ordinate space. In the analysis of the pendular clocking mode presented in the preceding subsection,  $\tau_0$  was regressed on  $m$  and  $l$  with  $K$  constant and  $G$  varying. The exponents thus obtained defined the time scales for an equipotential line in the  $K \times G$  space. These equipotential lines are of two kinds: horizontal lines parallel to the  $G$  axis representing constant  $K$  and vertical lines parallel to the  $K$  axis representing constant  $G$ . Across the horizontal equipotential lines we saw, in Fig. 2, that  $M_{exp}$  and  $L_{exp}$  varied systematically. This variation is identified in the depiction in Fig. 4 of the  $K \times G$  space by  $F(K)$  and  $f(K)$ , respectively. Also identified in the depiction of the  $K \times G$  space is how time scales to mass and length for constant  $K/G$  ratios. For any line through the space maintaining a constant ratio of  $K$  to  $G$ ,  $M_{exp} = 0$  and  $L_{exp} = 0.5$ . If  $K$  is a constant multiple of  $G$ , then the mass term cancels. The behavior of these exponents

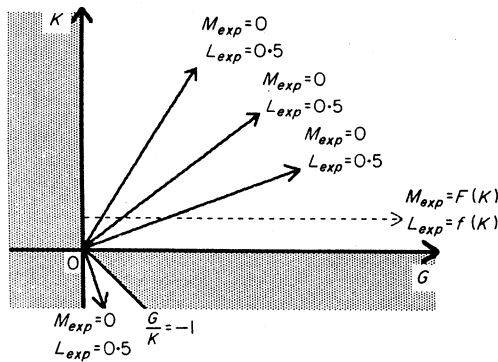


FIG. 4. The  $K \times G$  co-ordinate space. For systems that lie on a constant  $K/G$  trajectory, multiple regression of periodic time on mass and length renders  $M_{exp} = 0$  and  $L_{exp} = 0.5$ . For systems that lie on a constant  $K$  trajectory, regression analysis reveals that the exponents depend on the value of  $K$  (and the length scale). Shaded areas represent regions in which equation (2) is inapplicable. Although  $-G$  values are not possible,  $-K$  values are possible. There is, therefore, a small region of constant  $-K/G$  trajectories. The upper bound on this region is at  $-K = G$ .



in the  $K \times G$  space was evaluated with periodic times generated by equation (2) for 49  $m, l$  pairings and 33  $K/G$  ratios.

#### THE $K \times G$ SPACE WITH MASS AND LENGTH CORRELATED

We should now qualify the  $K \times G$  space just described. It is the co-ordinate space for the pendular, clocking mode when that mode is assembled over systems for which variations in mass and variations in length are uncorrelated or uncoupled—such as the wrist-pendulum systems in the experiments of Kugler & Turvey (1987). In the more typical biological instances of this mode,  $m$  is allometrically related to  $l$ . Over a broad spectrum of animals the allometric relation is found to be  $m \propto l^3$ , in accordance with geometric similarity (Peters, 1983). A number of students of allometry, however, are more committed to an  $l^4$  scaling, as follows from elastic similarity (Calder, 1984; Economos, 1982; McMahan, 1985). It is a simple enough matter to generate periodic timing data through the pendular, clocking mode equation with the pairings of masses and lengths constrained according to either of the preceding allometries. In the resultant  $K \times G$  space for  $m \propto l^3$ , any trajectory for which  $K/G$  is constant yields the following single-variable regression pattern:  $M \text{ exp} = 0.166$ ,  $L \text{ exp} = 0.5$ . The single variable regression pattern for constant  $K/G$  with  $m \propto l^4$  is:  $M \text{ exp} = 0.125$ ,  $L \text{ exp} = 0.5$ . More generally, whenever a scaling relation between mass and length,  $m \propto l^z$ , is embedded in the pendular clocking mode equation, it will always be the case that a constancy of  $K/G$  will constrain the single-variable linear regressions of  $\tau_0$  to an  $L \text{ exp}$  of 0.5 and an  $M \text{ exp}$  of  $0.5/z$ . For the two-variable regression the outcome for both mass-length relations is the same as when mass and length are uncorrelated magnitudes:  $M \text{ exp} = 0$ ,  $L \text{ exp} = 0.5$ .

Figures 5 and 6 show the dependence of  $M \text{ exp}$  and  $L \text{ exp}$  on  $K$ . With mass scaling as (a)  $l^3$  and (b)  $l^4$ , 45  $m, l$  pairs were used to generate, via the equation of the pendular clocking mode, 45 periodic times for each of 40 values of  $K$ . The obtained periodic times were then regressed on mass and on length separately (the perfect correlation between the two quantities built into the simulation ruled out multiple regression). Two different ranges of mass and length were examined. The ranges correspond approximately to the size ranges of (a) the limbs of large quadrupeds and (b) the wings of large birds. Figure 5 shows how the exponents behave as a function  $K$  under the  $m \propto l^3$  constraint; Fig. 6 shows how the exponents behave as a function of  $K$  under the  $m \propto l^4$  constraint. Evidently, the dependency on  $K$  of the mass-based and length-based time scales varies with range of sizes and with the particular relation of mass to length.

#### HOMOGENEITY AND INHOMOGENEITY IN THE SCALING OF MASS TO LENGTH

In allometric analyses it is customary to assume that for the different sized and different shaped animals under consideration, the relation of mass to length is constant. Here we compare the consequences of a constant scaling of mass to length and a variable scaling of mass to length. We look at the time scales for periodic

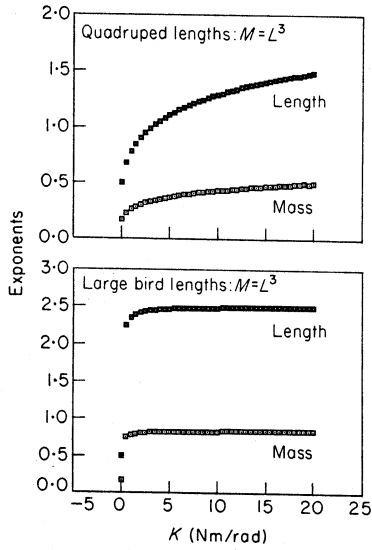


FIG. 5. The dependencies of  $M$  exp and  $L$  exp on  $K$  when  $m \propto l^3$ . Upper panel is for length scale of quadruped limbs. Lower panel is for length scale of large birds' wings.

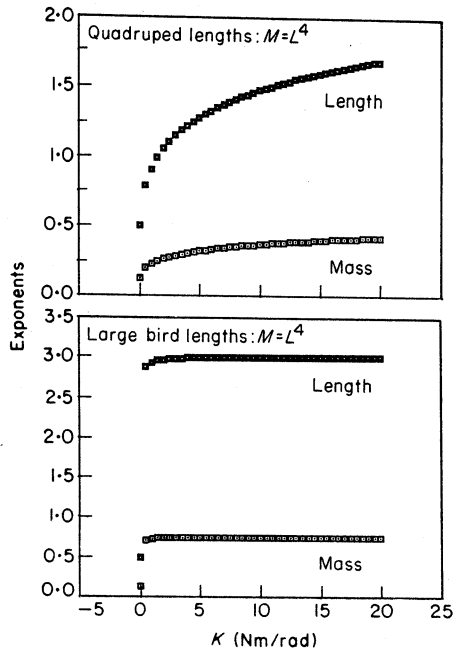


FIG. 6. The dependencies of  $M$  exp and  $L$  exp on  $K$  when  $m \propto l^4$ . Upper panel is for length scale of quadruped limbs. Lower panel is for length scale of large birds' wings.

times generated by the pendular clocking mode equation when the masses and lengths entered into the equation do and do not conform to a constant relation. The scalings of  $\tau_0$  to  $m$  and to  $l$  for a constant relation between  $m$  and  $l$  are shown in Fig. 7. The scalings for an inconstant relation are shown in Fig. 8.

In sum, we have developed four closely related arguments that are of significance to understanding the comfortable temporal behavior of coupled wrist-pendulum systems: (1) two wrist-pendulum systems in absolute co-ordination (rhythmically moving at the same tempo and with a constant phase relation) comprise a virtual single system, defined by single mass and length magnitudes; (2) in the steady state the periodic timing of virtual single wrist-pendulum systems is governed by the

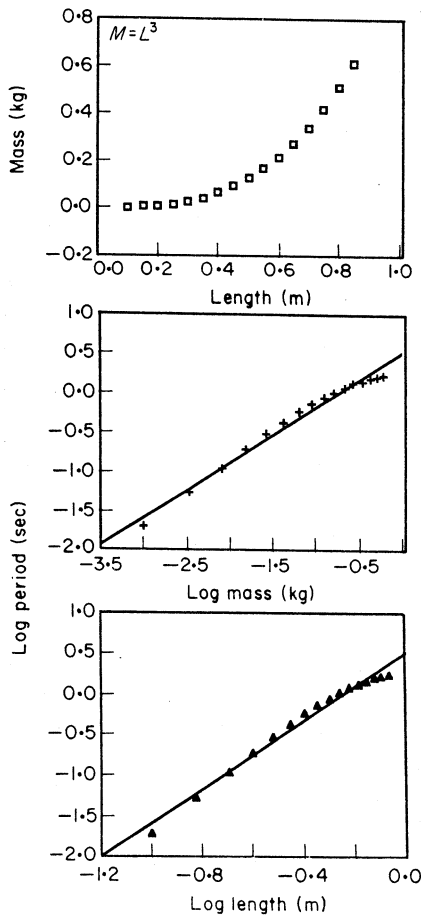


FIG. 7. The scaling of periodic time to mass and length when the relation between mass and length is constant. Periods are generated by equation (2).

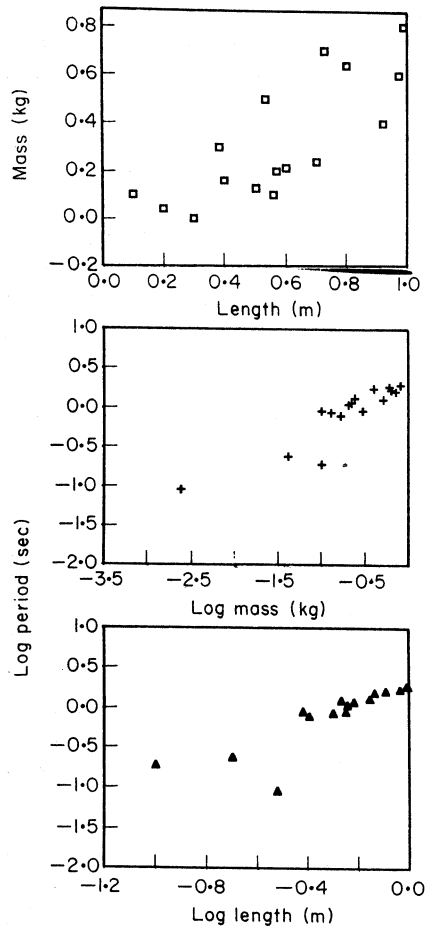


FIG. 8. The scaling of periodic time to mass and length when the relation between mass and length is variable. Periods are generated by equation (2).

pendular clocking mode equation, equation (2); (3) the mass-based and length-based time scales, or time allometries, are set intrinsically by equation (2) as constrained by the relation of mass to length; and (4) a set of virtual single wrist-pendulum systems will be on the same time scale if and only if (a) the geometry of these systems—the relation of mass to length—is constant and (b) the effective elastic potential  $K$  of these systems is constant.

#### Effects on Empirical Time Scales of Nonuniformity in the Scaling of Mass of Length

We conducted six experiments to evaluate the claim that rhythmic systems will share a common time allometry only if they share a common mass-to-length scaling (point 4(a) above). In each experiment reported, each of three subjects produced a comfortable, 180 degrees out-of-phase, rhythmic movement for either 11 coupled

wrist-pendulum systems (Experiments 1 and 6) or eight coupled wrist-pendulum systems (Experiments 2-5). The number of trials per system was either six or eight depending on the experiment. A trial's duration was of the order of 20 sec (for details on data collection methods see Kugler & Turvey, 1987; Turvey *et al.*, 1986). A given system's period for a given subject was defined by the mean period of the trials. Experiments were run approximately 3 months apart with the same three subjects in each experiment. In the experiments of Kugler & Turvey (1987),  $m$  and  $l$  were uncorrelated. Of the six experiments to be reported here,  $m$  was related to  $l$  through a well-defined power formula in three experiments (1, 5 and 6); in the other three experiments (2, 3 and 4) the proportionality of  $m$  to  $l$  was varied nonuniformly among the systems.

Figure 9 presents the data from Experiment 2. The upper panel shows the relation of mass to length for the set of virtual single wrist-pendulum systems examined.

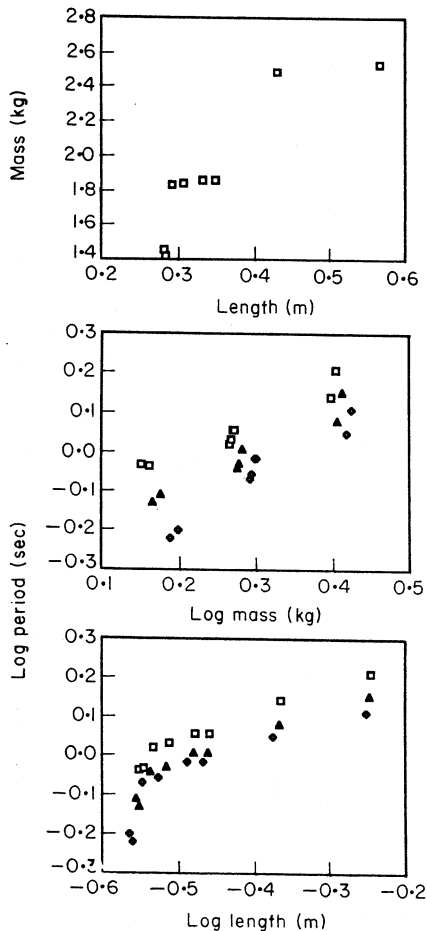


FIG. 9. Data on the three subjects under the conditions of Experiment 2 in which the relation between mass and length was not uniform across the wrist-pendulum systems. Key: □ S1, ▲ S2, ◇ S3.

Because subjects differed in body mass and because body mass enters into the computation of a wrist-pendulum system's magnitudes there was a mass-length relation defined for each subject. The mass-length relation was nearly identical for each subject, however, given that the pendulum shafts and pendulum weights were identical for each subject. It is sufficient, therefore, to show the relation for one subject (Subject 1). As can be seen, in Experiment 2  $m$  and  $l$  related inconsistently. The middle panel shows the mapping of log periodic time on log mass for each subject. The lower panel shows the mapping of log periodic time on log length for each subject. Inspection of the three panels of Fig. 9 reveals that inhomogeneities in the time scales reflected inhomogeneities in the mass-to-length scaling; the experimental data are consonant with the pattern of results produced by the pendular clocking mode equation under the conditions of a nonuniform mass-to-length relation (see Fig. 8). Figures 10 and 11 present the same three mappings for

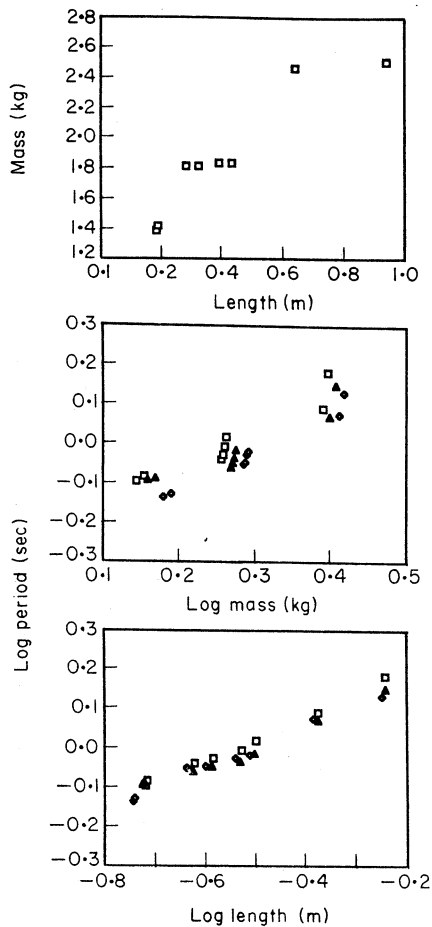


FIG. 10. Data on the three subjects under the conditions of Experiment 3 in which the relation between mass and length was not uniform across the wrist-pendulum systems. Key as in Fig. 9.

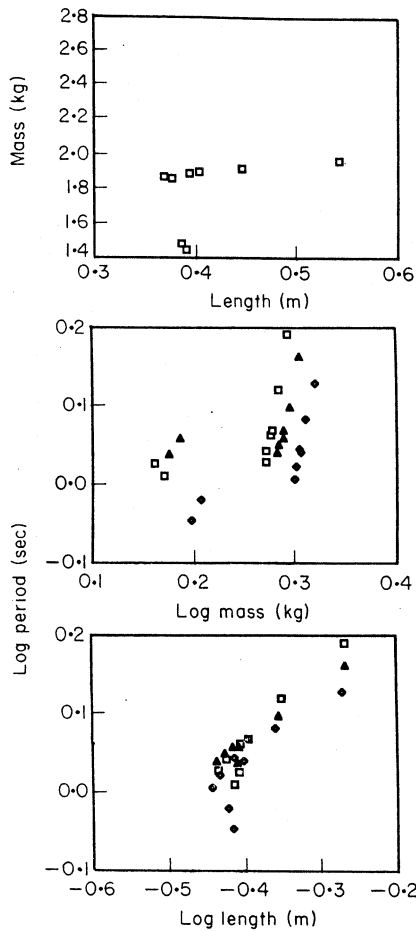


FIG. 11. Data on the three subjects under the conditions of Experiment 4 in which the relation between mass and length was not uniform across the wrist-pendulum systems. Key as in Fig. 9.

Experiments 3 and 4 and reveal the same sensitivity of wrist-pendulum systems' time allometries to variance in the scaling of mass to length.

In Figures 12-14 the three mappings are depicted for the experiments in which there was a single well defined relation between the magnitudes of mass and length, namely, Experiments 1, 5, and 6. In each case it can be seen that the time allometries were well defined—as expected from the pendular clocking mode equation (see Fig. 12).

#### Effects on Empirical Time Scales of Different Values of $K$

We now wish to use the data from Experiment 6 to address points 3 and 4(b) above. The pendular clocking mode equation will prescribe  $m$  and  $l$  exponents as single-valued functions of  $K$  given an invariant scaling of  $m$  to  $l$ . The power formulae

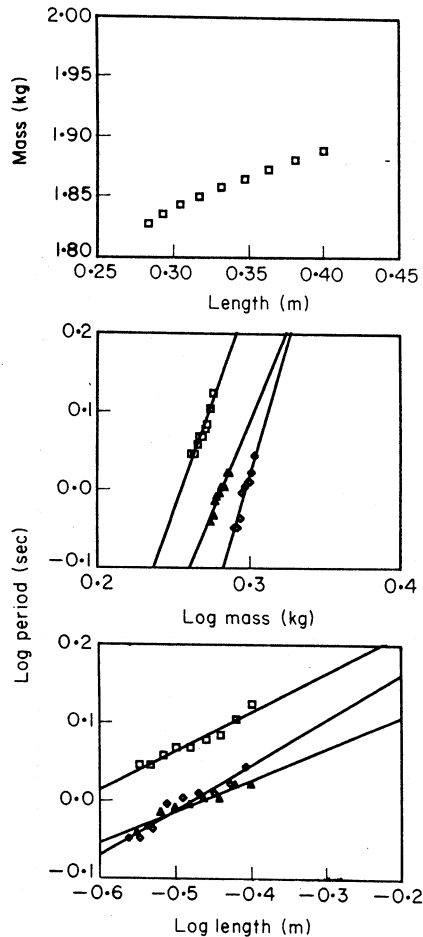


FIG. 12. Data on the three subjects under the conditions of Experiment 1 in which the relation between mass and length was uniform across the wrist-pendulum systems. Key as in Fig. 9.

relating  $m$  and  $l$  for the three subjects in Experiment 6 were, respectively,  $m = 1.596(l)^{0.082}$ ,  $r^2 = 0.980$ ;  $m = 1.644(l)^{0.074}$ ,  $r^2 = 0.979$ ;  $m = 1.717(l)^{0.074}$ ,  $r^2 = 0.978$ . These scaling equations were used in defining three sets of 49  $m, l$  pairs, one for each subject. Then, for each of 15 values of  $K$  in the range from  $-0.5$  to  $3.0$ , periodic times were generated through equation (2) for each  $m, l$  pair. The logarithmic values of these periodic times were then regressed onto the logarithmic values of the  $m$ s and the logarithmic values of the  $l$ s for each value of  $K$ . The results were functions relating  $M$  exp and  $M$  int (int = intercept from regression in logarithmic co-ordinates) to  $K$ , and functions relating  $L$  exp and  $L$  int to  $K$ , for each of the three power formulae relating  $m$  to  $l$  (that is, for each subject). We then went into the data of the experiment and for each subject computed, by equation (2), the  $K$  values associated with each of the 11 coupled wrist-pendulum systems examined in the



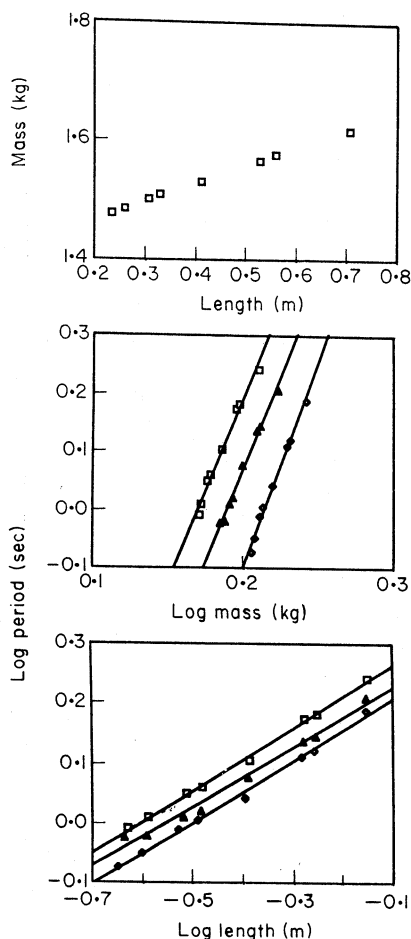


FIG. 13. Data on the three subjects under the conditions of Experiment 5 in which the relation between mass and length was uniform across the wrist-pendulum systems. Key as in Fig. 9.

experiment. The 11  $K$  values computed for a subject were not identical but many were closely similar. We proceeded to identify for each subject that range equal to one  $K$  within which fell the largest number of systems. Eight out of the 11 systems for Subjects 1 and 2, and seven out of the 11 systems for Subject 3, clustered together in a range of  $K$  values that was less than one. We then allowed that these particular systems be considered as operating with the same  $K$  value. Consequently, the mean of the range was used to identify, for each subject, a single  $K$  value for the time scales computed for the systems within the range. For Subjects 1, 2 and 3 these  $K$  values were  $-0.045$ ,  $0.65$  and  $1.76$  Nm/rad, respectively.

The results of the preceding analyses are presented in Fig. 15. We note that in each graph,  $L_{exp}$  and  $L_{int}$  are given as a function of  $K$  (that is, the exponent and the intercept of the regression of  $\log \tau_0$  on  $\log l$  are given for each of 15 values of

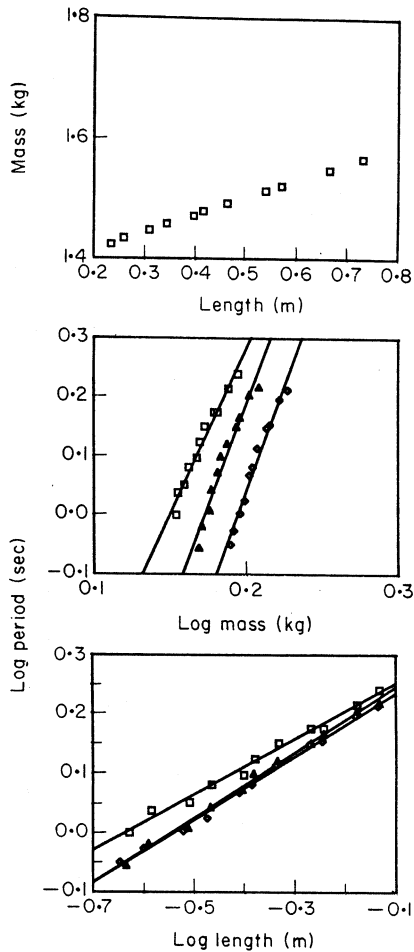


FIG. 14. Data on the three subjects under the conditions of Experiment 6 in which the relation between mass and length was uniform across the wrist-pendulum systems. Key as in Fig. 9.

K). These functions are those expected for a system in the pendular clocking mode—as defined by equation (2)—under a given  $m$ -to- $l$  scaling. Across the three graphs the  $m$ -to- $l$  scaling differs, as noted in the power formula given above, corresponding to differences among the three subjects in body mass. Superimposed upon the predicted  $L_{exp}$  and  $L_{int}$  functions in each of the three graphs are the observed  $L_{exp}$  and  $L_{int}$  values obtained for the representative  $K$  value at which the subject operated. As can be seen, the observed length-based time allometry of each subject matches the length-based time allometry that would be exhibited by a hybrid mass-spring/simple pendulum system (Fig. 1) under the same  $m$ -to- $l$  scaling and the same constant  $K$ . Figure 16 represents the corresponding graphs for  $M_{exp}$  and  $M_{int}$ . Although the predicted and observed mass-based time allometries match

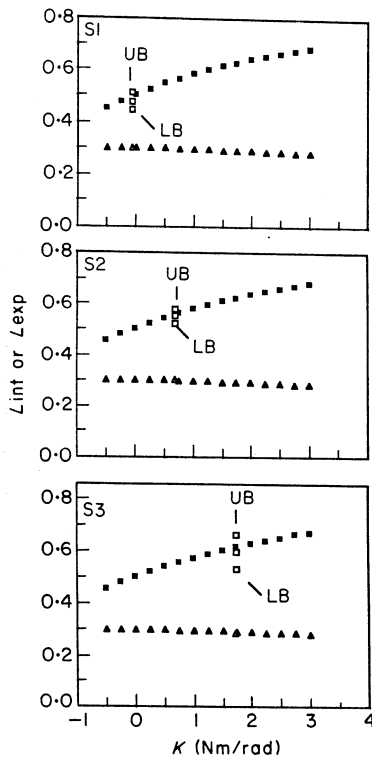


FIG. 15. The relations between  $L_{exp}$  and  $K$  and  $L_{int}$  and  $K$  for each of the three subjects under the conditions of Experiment 6. Key: ■, ▲ predicted; □, △ observed; UB = upper bound, LB = lower bound.

less well, it is nonetheless the case that the fit is good, reinforcing the dynamic analogy between the rhythmic systems assembled by a subject over neural, metabolic and muscular processes and the physical system given by equation (2) and depicted in Fig. 1.

### Quadruped Locomotion's Time Scales and Gaits Interpreted in the Gravitational-Elastic Co-ordinate Space

The pendular, clocking mode is a simple dynamical regime. In living systems it is manifest as the assembling of one potential, through local dissipative processes, in order that another potential, provided freely and universally, can be exploited. The preceding arguments and analyses have established that equation (2) accommodates the major observations on this regime as instanced by wrist-pendulum systems in absolute co-ordination. Given that the design for this dynamical regime is so restricted, however, it is likely to be the case that equation (2) addresses all instances. Terrestrial, mammalian locomotion—walking, trotting and cantering (Pennycuik, 1975)—typifies the pendular, clocking mode. It can be hypothesized, therefore, that

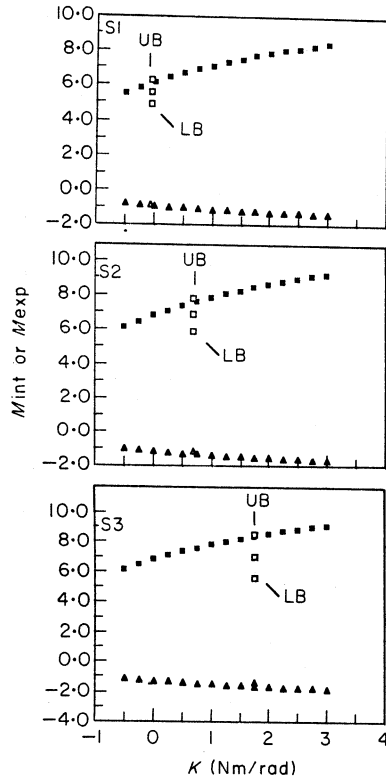


FIG. 16. The relations between  $M_{exp}$  and  $K$  and  $M_{int}$  and  $K$  for each of the three subjects under the conditions of Experiment 6. Key as in Fig. 15.

terrestrial locomotion's characteristic, universal properties follow directly from the structure of equation (2).

Figure 17 presents in double logarithmic co-ordinates the periodic times of the three major quadruped gaits as a function of (a) hindleg length and (b) body mass. The periodic times and leg lengths are derived from Pennycuik (1975); the body masses are from Garland (1983). A table summarizing these data can be found in Kugler & Turvey (1987, Chapter 8). One-variable regression analyses reveal that, in each gait, periodic time scales close to length to the  $1/2$  power; walking,  $L_{exp} = 0.486$  (95% confidence limits, 0.373, 0.598); trotting,  $L_{exp} = 0.512$  (95% confidence limits, 0.123, 0.900); cantering,  $L_{exp} = 0.446$  (95% confidence limits, 0.284, 0.608). They also reveal that, in each gait, periodic time scales close to body mass to the  $1/6$  or  $1/8$  power: walking,  $M_{exp} = 0.157$  (95% confidence limits, 0.103, 0.21); trotting,  $M_{exp} = 0.106$  (95% confidence limits,  $-0.067$ , 0.279, but nonsignificant); cantering,  $M_{exp} = 0.120$  (95% confidence limits, 0.047, 0.193).

Two further properties can be noted. When multiple regression analyses are performed on the data of the gaits,  $L_{exp}$  is highly significant and close to 0.5 but  $M_{exp}$  is nonsignificant and closer to 0 than to 0.167 or 0.125. The multiple regression

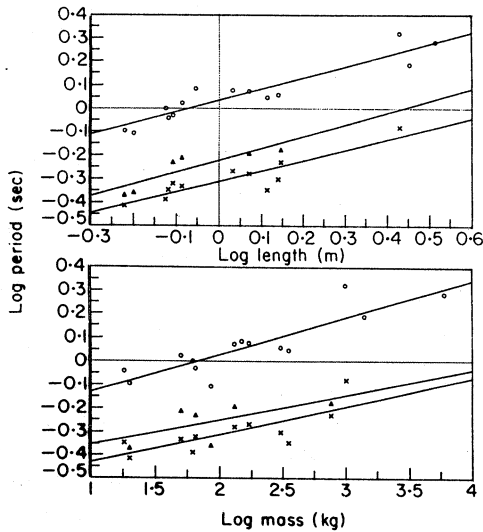


FIG. 17. Log periodic time against log hindleg length (upper panel) and log body mass (lower panel) for quadruped walking, trotting and cantering. Key:  $\circ$  walking,  $\blacktriangle$  trotting,  $\times$  cantering.

reaches significance only for the walk and the canter (the trot data have too few degrees of freedom). For walking,  $r^2(13) = 0.881$ ,  $P < 0.0001$  with  $M \text{ exp} = -0.005$ ,  $P = 0.926$  and  $L \text{ exp} = 0.500$  (95% limits, 0.151, 0.849),  $P = 0.009$ . For cantering,  $r^2(10) = 0.829$ ,  $P < 0.009$  with  $M \text{ exp} = -0.051$ ,  $P = 0.396$  and  $L \text{ exp} = 0.598$  (95% limits, 0.173, 1.022),  $P = 0.01$ . The multiple regression analyses strongly imply that the scaling of time to mass evident in the single variable regressions of Fig. 17 is due simply to the relation of body mass to leg length. The beta weights in a multiple regression reveal the unique contribution of each of the independent variables to the variance of the dependent variable. Consequently, the preceding analyses indicate that body mass does not account uniquely for the variance in periodic timing. For the data represented in Fig. 17,  $M \propto L^{2.77}$  with an  $r^2 = 0.89$ . But given that the allometric relation is just as valid when expressed as a proportional dependency of length on mass,  $L \propto M^{0.361}$ , the question arises as to why  $M \text{ exp}$  vanishes rather than  $L \text{ exp}$ —that is, why leg length accounts for the variance in period rather than body mass?

Further, when the four limbs are transformed into a virtual single limb of length  $l$  (using the methods by which two coupled wrist-pendulum systems are converted into a virtual single system), analysis reveals that quadruped walking, trotting and cantering approximate closely the periods of a freely oscillating pendulum of length  $l/2$ ,  $l/7$  and  $l/10$  respectively (Kugler & Turvey, 1987). That is to say, walking periods follow from  $\tau_0 = 2\pi(l/2g)^{1/2}$ , trotting periods follow from  $\tau_0 = 2\pi(l/7g)^{1/2}$ , and cantering periods follow from  $\tau_0 = 2\pi(l/10g)^{1/2}$ .

Each of the preceding properties can be derived from the equation of the pendular, clocking mode—equation (2). Looking again at the locomotory data depicted in

Fig. 17, the observation of colinearity among the periods of animals that differ in size and shape points to an invariant. That there are three distinct colinearities suggests that there are three distinct invariants. If the pendular, clocking mode is universally described by equation (2), then the shape- and size-independent quantity characterizing a gait must be defined within the equation. Is  $K$  the underlying invariant? This hypothesis is easily dismissed. The mass of an oscillating leg was computed as 7% of body mass; the length was computed as the length of an equivalent simple pendulum. For the three gaits the computed mean values and standard deviations for  $K$  (in Nm/rad) were, respectively, 1073.61 and 2769.02 for walking, 639.42 and 1194.22 for trotting and 1906.46 and 2970.45 for cantering. Across walkers  $K$  ranged from 6.84 to 10 209.22; across trotters  $K$  ranged from 37.04 to 3063.10; and across canterers  $K$  ranged from 46.69 to 9859.99. Is  $G$  the underlying invariant? This hypothesis is similarly easy to dismiss: by definition  $G(=mlg)$  varies markedly with animal size. The only remaining possibility is that, across locomoting animals of different shapes and sizes, it is the ratio of  $K$  to  $G$ , a dimensionless quantity, that is constant, with a different dimensionless constant for each gait. For example, if  $K/G = 1$  then, equation (2) would be transformed as follows:

$$\tau_0 = 2\pi[m l^2 / (m l g + k b^2)]^{1/2} = 2\pi(m l^2 / 2 m l g)^{1/2} = 2\pi(l / 2g)^{1/2}. \quad (9)$$

Equation (9) is the equation for walking noted above. Similarly, if  $K/G = 6$  and  $K/G = 9$  then  $\tau_0 = 2\pi(l/7g)^{1/2}$  and  $\tau_0 = 2\pi(l/10g)^{1/2}$ , respectively, which are the equations noted above for trotting and cantering. Whether or not these particular equations, these particular fractions of  $l$  or multiples of  $g$  (and integer fractions of multiples at that), are correct is immaterial to the larger point being made. What makes the periods of a gait cohere across animals of different sizes and shapes is the fact that the elastic restoring torque assembled by each animal, namely  $K$ , is the same constant multiple of the gravitational restoring torque associated with the magnitudes of each animal, namely  $G$ . Computation of the  $K/G$  ratios yielded mean values (standard deviations in parentheses) of 1.195 (0.428) for the walk; 6.059 (1.276) for the trot; and 9.744 (2.233) for the canter. Estimating the ratios from the regression of  $K$  on  $G$  yielded 1.244 for walking 6.908 for trotting and 8.665 for cantering.

Finally, we address the time scales of quadruped locomotion revealed through single and multiple regression by reference to the preceding discussion of the properties of the  $K \times G$  co-ordinate space when mass and length are correlated quantities. The first feature to be noted is that for constant  $K/G$ , simple regression yields  $L \text{ exp} = 0.5$  and  $M \text{ exp} = 0.5/z$ , where  $z$  is given by  $m \propto l^2$ . Recall that for the locomotion data of Fig. 17,  $L \text{ exp}$  is in the vicinity of 0.5 and  $M \text{ exp}$  is in the vicinity of 0.125 and 0.167. The second feature to be noted is that for any line through the space maintaining a constant ratio of  $K$  to  $G$ ,  $M \text{ exp} = 0$  and  $L \text{ exp} = 0.5$  when  $\tau$  is regressed simultaneously on  $m$  and  $l$ . This is also true of the multiple regressions conducted on the walk and canter data of Fig. 17. Although the latter regressions were computed on body mass, it can be assumed that the pattern of results holds for leg mass. Leg mass data for quadrupeds was not available to us.

## Large Birds

Suppose that the pendular, clocking mode is a movement organization that applies universally wherever biological masses oscillate about a fixed point relative to a torsional stiffness due to gravity and a torsional stiffness due to the elasticity of biological tissue. By this supposition flying—by birds, hummingbirds and insects—is a pendular, clocking organization. The closely parallel functions shown in Fig. 18 of  $\log \tau$  against  $\log l$  for wrist-pendulum systems, quadrupeds walking, trotting and cantering, and large birds in flight are consonant with this hypothesis.

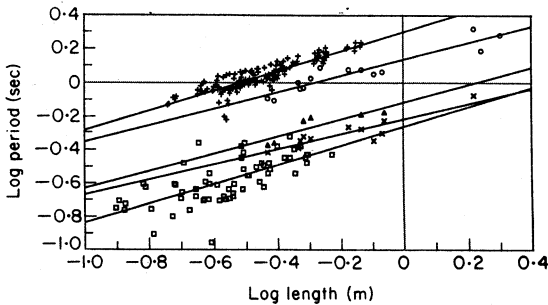


FIG. 18. Similar dependency for periodic time on length for wrist-pendulum activity, quadruped gaits and the flying of large birds. For all but the large birds, lengths are estimated equivalent simple pendulum lengths. Wrist-pendulum data are the complete data set of the six experiments. Key: as above and + wrist-pendulum,  $\square$  large birds.

The allometry of flying should conform, therefore, to the pendular, clocking mode equation, equation (2). One prediction is that for any body of allometric data connecting wing periods in flight to masses and lengths, if  $L \text{ exp}$  equals 0.5 and  $M \text{ exp}$  equals  $0.5/z$  ( $z$  defined as above) with simple regression, and  $M \text{ exp}$  vanishes with multiple regression, then the  $K/G$  values across the individual animals must be identical or very similar. To the extent that  $L \text{ exp}$  does not equal 0.5 etc., then the  $K/G$  values must be heterogeneous rather than homogeneous.

Measurements on 37 large birds (ranging in body mass from 0.062 to 2.69 kg and ranging in wing length from 0.125 to 0.497 m) were obtained from Meinertzhagen (1955) and Magnan (1922), as presented, respectively, in Tables 13 and 15 of Greenewalt (1962). Table 13 provides wing periods and wing lengths; Table 15 provides, among other things, wing and body masses and wing lengths. To assign masses from Table 15 to a bird in Table 13 we required that the wing length estimates given for that bird did not differ by more than 0.03 m in the two tables. (Thus, for example, wing period of the cormorant—*Phalacro corax carbo*—was not included because the wing length estimates were 0.350 and 0.424 m in Table 13 and Table 15, respectively). Simple regression identified the timing relations:  $\tau_0 \propto \text{wing mass}^{0.144}$  ( $r^2 = 0.294$ ,  $P < 0.001$ ; intercept at 1 kg, 2.529 sec) and  $\tau_0 \propto \text{wing length}^{0.540}$  ( $r^2 = 0.515$ ,  $P < 0.0001$ ; intercept at 1 m, 0.518 sec) and the wing mass relations:  $\text{wing mass} \propto \text{body mass}^{1.056}$  ( $r^2 = 0.903$ ,  $P < 0.0001$ , 95% confidence limits on exponent of 0.937, 1.175; intercept at 1 kg equal to 0.150 kg) and  $\text{wing mass} \propto \text{wing length}^{2.63}$

( $r^2 = 0.863$ ,  $P < 0.0001$ , 95% confidence limits on exponent of 2.267, 2.983; intercept at 1 m equal to 2.056 kg).

The observed allometries approximate closely those expected if  $K/G$  for large birds is reasonably homogeneous. With respect to timing's dependence on the length of the oscillating wing, the expected value would be  $L \exp = 0.5$ . The observed value was  $L \exp = 0.54$  (95% confidence limits, 0.36, 0.72). (If one relaxes the requirement of evaluating the wing length time allometry only for large birds for which measures on each of wing mass, wing length, body mass and wing period can be found, then period can be regressed on wing length for 62 cases:  $r^2 = 0.469$ ,  $P < 0.0001$ ,  $L \exp = 0.577$  between 95% limits of 0.42, 0.734; intercept at 1 m, 0.546 sec). With respect to timing's dependence on the mass of the oscillating wing, the expected value would be  $M \exp = 0.5/2.63$ , that is,  $M \exp = 0.190$ . The observed value was 0.144 (95% confidence limits, 0.068, 0.221). If geometric similarity held perfectly (wing mass scaled as the cube of wing length) then the expected and observed values of the wing mass exponent would be even more similar—0.166 compared with 0.144. The low  $r^2$ s of the timing relations relative to the wing mass relations are most likely due to a basic difference in the accuracy of the two kinds of data. Measures of wing period in flying birds will be less precise (see Rayner, 1979) than measures of wing mass (body mass, wing length) in freshly killed birds. The 95% confidence limits on the two timing relations were 0.07 (lower) and 0.22 (upper) for  $\tau_0 \propto$  wing mass and 0.36 (lower) and 0.72 (higher) for  $\tau_0 \propto$  wing length. With respect to the wing mass scalings, the 95% limits on the body mass exponent were 0.94 and 1.18 and on the wing length exponent they were 2.27 and 3.0.

The other expected outcome of  $K/G$  homogeneity was not approximated, however: simultaneous regression of wing period on wing mass and wing length yielded a significant negative mass exponent of  $-0.244$  ( $P = 0.003$ , 95% limits  $-0.397$ ,  $-0.091$ ) and a significant positive length exponent of 1.18 ( $P = 0.001$ , 95% limits 0.747, 1.613). A similar result followed from regressing wing period on body mass and wing length: a significant negative mass exponent of  $-0.204$  ( $P = 0.0004$ , 95% limits  $-0.304$ ,  $-0.104$ ) and a significant positive length exponent of 0.961 ( $P = 0.0001$ , 95% limits 0.706, 1.215). To compute the  $K/G$  dimensionless quantities for the 37 large birds, wing length was assumed to be equivalent to  $l$  in equation (2) and wing mass was taken as  $m$ . This resulted in a rough approximation of the  $K/G$  ratios with a mean value of 15.323, a standard deviation of 6.181, and a range of 3.183–27.711. Comparison of these values with those reported above for the quadrupeds suggests that large birds in flight are not as homogeneous on the  $K/G$  dimension as are quadrupeds in the performance of a given gait. The coefficient of variation (standard deviation/mean) was 0.358 and 0.229 for the walking and cantering of quadrupeds, respectively, and 0.403 for the flying of large birds. The imprecision of the temporal measure for birds (relative to that for quadrupeds) should be cited as one possible contributing factor to this greater variability in the birds'  $K/G$  quantities. Another source of variability may lie in design differences among large birds that amount to very different mass-to-length scalings. Greenewalt (1975) distinguishes three design models: the "passeriform", the "shorebird" and the "duck" (each model is named by the most prominent bird group that it embraces).



Of the 37 large birds included in the preceding analyses, 16 belong to the "passeriform" model, eight belong to the "shorebird" model and six belong to the "duck" model. The  $K/G$  means and standard deviations for the three models were "passeriform" 12.86, 4.01; "shorebird" 15.09, 4.58; and "duck" 24.32, 2.73. The coefficients of variation for the three models are, respectively, 0.312, 0.304, 0.112.

Although the data base is limited, the  $K/G$  contrast among the three models suggests that the differences among them may be similar, in dynamical terms, to the differences among the quadruped gaits. By using "model", therefore, as a categorical variable in the multiple regression (see Pedhazur, 1981) of wing period on mass and length we can homogenize effectively the data with respect to  $K/G$ . This should render  $M \exp$  insignificant and  $L \exp$  very close to 0.5, as predicted by the pendular, clocking mode equation. The regression of log period on log wing length, log body mass and model as a categorical variable proved significant,  $r^2 = 0.779$ ,  $P < 0.001$ . Neither of the continuous variables, log body mass and log wing length, interacted with the model variable (model  $\times$  log length,  $F(2, 24) = 0.828$ , and model  $\times$  log mass,  $F(2, 26) = 0.179$ ). The effect of model, however, was significant:  $F(2, 30) = 3.87$ ,  $P < 0.05$ . With the variance due to model (and, by argument, the variance in  $K/G$ ) partialled out, body mass proved to be insignificant,  $M \exp = -0.038$ ,  $P < 0.583$ , and wing length proved to be significant and in the vicinity of the expected  $1/2$  power,  $L \exp = 0.549$ ,  $P = 0.004$ , (95% limits 0.197, 0.901). Repeating the analysis with wing mass yielded the same pattern of results:  $M \exp = -0.057$ ,  $P = 0.462$ , and  $L \exp = 0.619$ ,  $P = 0.01$  (95% limits, 0.163, 1.075).

In sum, when differences in the designs of large birds are taken into account (Greenewalt, 1975), multiple regression reveals that, of the two variables of length and mass, only length affects wing frequency significantly. This result, together with the outcomes of the simple regressions, suggest that the wing frequencies of large birds can be reasonably well understood as expressions of the pendular clocking model defined by equation (2). It should be pointed out that this conclusion does not provide insights into flight techniques or flight efficiencies. It is purely a conclusion about the movement organization underlying the period of wing beats and is of little relevance, thereby, to issues of how beating wings produce propulsion or lift.

### Small Birds and Hummingbirds

We now wish to highlight the fact that the length-based time allometry of large birds—in which wing beat period scales as length to approximately the  $1/2$  power—is not reproduced in other birds of smaller stature. Data on eight passerines with wing lengths of less than 0.125 m (range 0.065–0.120 m) are to be found in Greenewalt (1962, Table 10). The simple regression of log periodic time on log wing length ( $r^2 = 0.868$ ,  $P < 0.001$ ) reveals a length exponent for these small passerines of 1.198 (95% confidence limits of 0.731, 1.664; intercept at 1 m, 0.926 sec). This length exponent is closely similar to that of hummingbirds. Greenewalt (1962, Tables 9 and 10) provides wing period and wing length data on 70 hummingbirds (wing mass data, unfortunately, are not provided). Simple regression ( $r^2 = 0.736$ ,  $P < 0.0001$ )

performed on the logarithms of these quantities yields  $L \exp = 1.190$  (95% confidence limits of 1.017, 1.362; intercept at 1 m, 1.030 sec). We present the hummingbird data in Fig. 19. An important feature of these data is the presence of a highly significant quadratic component; linear component,  $P = 0.03$ , quadratic component,  $P = 0.005$ . The polynomial regression, rather than the linear regression, is identified in the figure. The nonlinear nature of the hummingbird data implies that the rate of change of log period with respect to log wing length is not constant—the rate slows as the wings lengthen. Collectively, the relations between wing period and wing length for large birds, small passerines and hummingbirds suggest a function in log period  $\times$  log length space that is changing rate (continuously from an exponent of 1 to an exponent of 0.5) in the vicinity of lengths characteristic of birds and hummingbirds. (This suggestion is pursued below, following a detailed analysis of time allometry in the range of lengths occupied by insects.)

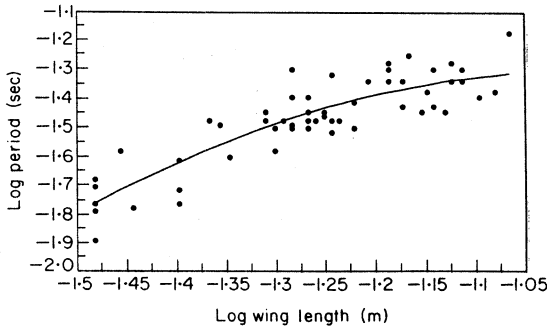


FIG. 19. Log wing beat period against log wing length for hummingbirds. The second-order polynomial regression is presented.

Another feature of the hummingbird data warrants careful consideration. The simple regression of log period on log body mass reveals a noticeable departure from the proposed fundamental physiological time scale:  $\tau_0 \propto \text{body mass}^{0.644}$  ( $r^2(57) = 0.595$ ,  $P < 0.0001$ , 95% confidence limits 0.517, 0.81; intercept at 1 kg, 0.258 sec). Wing length scales similarly to body mass:  $\text{wing length} \propto \text{body mass}^{0.601}$  ( $r^2(57) = 0.844$ ,  $P < 0.0001$ , 95% confidence limits 0.532, 0.670; intercept at 1 kg, 0.345 m). Is the odd time scale with respect to body mass simply due to the proportioning of wing length to body mass? Multiple regression suggests that it is:  $r^2(57) = 0.728$ ,  $P < 0.0001$ ;  $M \exp = -0.064$ ,  $P = 0.678$ ;  $L \exp = 1.211$ ,  $P = 0.0001$ , 95% confidence limits, 0.742, 1.68. Multiple regression also suggests—given that  $L \exp$  is not equal to 0.5—that the hummingbird data are not homogeneous with respect to  $K/G$ . In the absence of a further parameter, of the nature of “model” in the large bird analysis, the variance due to  $K/G$  cannot be partialled out and the appropriateness of equation (2) cannot be evaluated fully.

In sum, it appears that for hummingbirds periodic time scales to wing length (close to, but in excess of, the first power) and not to body mass. There may be nothing especially odd about hummingbird wing beat period. (If wing mass measures

were available then it may well turn out that periodic time scales as wing mass close to the 1/3 power.) What is beginning to look odd, however, is the effort to express time in terms of body mass.

### Further Considerations of the Pendular Clocking Mode

There is some reason to believe that wing frequencies in birds, hummingbirds and insects are constant across the varied conditions of flight (Greenewalt, 1960, 1975; Sotavalta, 1952, 1954). (For contrary evidence in birds, see Pennycuik, 1968, and Tucker, 1972.) This constancy suggests to Greenewalt (1960) that wing frequencies can be explained as the characteristic frequencies or eigenfrequencies of driven damped oscillators. The differential equation describing the (harmonic) motion of such oscillators is

$$I(d^2\phi/dt) + B(d\phi/dt) + Sb = F_0b \cos(2\pi/\tau), \quad (10)$$

where  $I$  is moment of inertia,  $B$  is the damping parameter,  $S$  is the harmonic restoring force,  $F_0$  is the amplitude of the driving force,  $\phi$  is the angular displacement,  $b$  is the mechanical advantage term associated with the point of application of  $S$  and  $F_0$  relative to the point of rotation,  $\tau$  is period and  $t$  is time. Applied to birds or insects, Greenewalt (1960) suggests that  $I$  is the moment of inertia of the wing and of the muscles, bones and tissues of the external skeleton that oscillate with the wing;  $B$  is the damping that arises from friction at the joints and between muscle fibers;  $F_0b$  is the magnitude of the moment exerted by the muscular driving force derived from muscle chemistry; and  $Sb$  is the restoring moment related to the elastic properties of muscle and other tissue. In Greenewalt's (1960) modeling of the oscillatory mechanism of flight, there is no gravitational contribution to the restoring moment. We will suggest below that Greenewalt's analysis represents a limiting case of the pendular, clocking mode—as body mass or length decreases, the restoring moment related to gravity becomes negligible in comparison with the restoring moment related to the elasticity of the body's tissues.

To continue Greenewalt's analysis, an elastic solid subjected to linear (uniaxial) tension or compression, will deform (within limits) according to Hooke's law

$$(l - l_i) = \Delta l = fl_i = EA_i, \quad (11)$$

where  $l$  is length,  $l_i$  and  $A_i$  are the initial length and initial cross-sectional area, respectively,  $f$  is the tensile force, and  $E$  is Young's modulus (with the dimensions of  $ML^{-1}T^{-2}$ ). From a consideration of the force-extension relation of elastic polymers, Greenewalt (1960) derives an expression for the elastic restoring force due to muscle elasticity, namely,  $S = El_0b\phi$ , where  $l_0$  is the length of unstrained muscle relative to the equilibrium position of  $\phi = 0$ . The characteristic period of the system described by equation (10), when free and undamped (that is, when  $B = 0$  and  $F_0 = 0$ ), can be expressed, therefore, as

$$\tau_0^2 = 4\pi^2 I / El_0b^2. \quad (12)$$

From standard considerations, Greenewalt (1960) argues that the muscular driving force  $F_0$  identified in equation (10) will be at a minimum (and, therefore, the energy

to sustain oscillation will be at a minimum), when  $F_0$  is in resonance with the characteristic period of the free, undamped system defined by equation (12).

The pendular clocking mode equation—equation (2)—differs from equation (12) in that the restorative moment is the sum of two terms,  $K$  and  $G$ . The pendular clocking mode equation is the same as equation (12), however, in that it defines the characteristic period of a free, undamped system.  $K$  and the quantity  $El_0b^2$ , identified as the restorative term due to tissue elasticity in equation (12), can be equated. The quantity  $K = El_0b^2$  refers to an elastic system that stores and releases kinetic energy with, presumably, low frictional losses. Given that  $E$  and  $b$  are constants for a biological system, it follows that, when operating in the pendular clocking mode, this elastic system can be varied only to the degree that  $l_0$  can be varied. As noted above, the available data suggest that, for a person assembling wrist-pendular clocking motions,  $K$  and, therefore,  $l_0$  may vary with  $I$ . The preceding ideas and observations are consistent with an important contemporary theory of movement control—Feldman's (1966a, 1966b, 1974, 1980, 1986) lambda model—which asserts that mammalian muscle, together with reflex and central control mechanisms, behaves like a nonlinear spring whose zero length (lambda) is a controllable parameter.

Insect wing beat period should be describable by equation (12)—which we should now recognize as equation (2) in the range of lengths in which  $G(=mIlg)$  becomes negligible, that is to say, when the space scale of the motions is too small for gravity to be a factor and the only source of restoring forces is the elastic system. In insects, the elastic system is constructed from at least three different materials or structures: (a) the solid skeletal cuticle of the thoracic box; (b) a typical elastomere in the form of the protein resilin; and (c) an elastic component in the myofibrils (Buchta & Weis-Fogh, 1956). Given the constancy of wing period, it is unlikely that the insect elastic system is controllable in the sense above. For purposes of insect flight a constancy of  $K(=El_0b^2)$  will suffice. Evidence that  $K$  is a constant, or very nearly so, for a given insect comes from Sotavalta (1952, 1954). Sotavalta (1952, 1954) conducted experiments (on members of a large variety of insect species) in which he reduced progressively the size of an insect's wings. After each reduction, the wing beat period and the moment of inertia of the residual wing segment were measured. A plot of  $\tau_0^2$  against  $I$  for two specimens of *Apis mellifica* is presented in Greenewalt (1960). The relation between the two quantities is linear. The slope of the linear relation is  $4\pi^2/K$  and the intercept defines the characteristic  $\tau_0^2$  of the muscle system alone.

Sotavalta's (1952, 1954) experiments with insects are paralleled by our experiments with humans. In the six experiments referred to above, each of three persons produced rhythmic movements with "limbs" that differed in moment of inertia from condition to condition (each condition was a different virtual single wrist-pendulum system). In the same way that Sotavalta's (1952, 1954) manipulation of clipping the wings permits the investigation of the relation between  $\tau_0^2$  and  $I$  within a single insect, our manipulation of varying the magnitude of hand-held pendulums permits the investigation of the relation between  $\tau_0^2$  and  $I$  within a single person. If the restoring term provided by the elastic system of the individual insect is constant

then equation (2) would predict a linear dependency of  $\tau_0^2$  on  $I$  as depicted in Greenewalt (1960). At the length scale of humans, where gravitational contributions are prominent, it is the case that if the restoring term provided by the elastic system of the individual person is constant, then equation (2) would predict a nonlinear dependency of  $\tau_0^2$  on  $I$ . The latter follows from the fact that  $G = mlg$  must be nonlinearly related to  $I$ .

Constancy of the elastic system's contribution is, however, not required for the foregoing linear and nonlinear predictions to hold. First, if  $K$  is not constant but subject to reasonably small variations about a mean state, then the mapping of  $\tau_0^2$  on  $I$  will still be linear and nonlinear for insect and human, respectively; the only

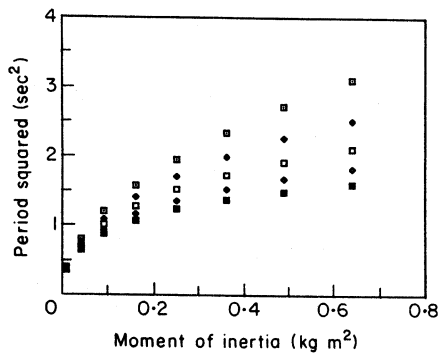


FIG. 20. Period squared as a function of moment of inertia for different values of  $K$  (expressed as multiples of moment of inertia). Functions are generated by equation (2). Key: □ 0.5  $I$ , ◆ 3.5  $I$ , ○ 6.5  $I$ , ◇ 9.5  $I$ , ■ 12.5  $I$ .

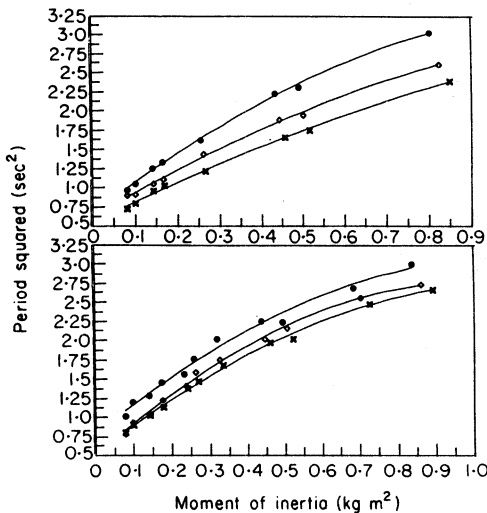


FIG. 21. Period squared plotted against moment of inertia for the three subjects under the conditions of Experiment 5 (upper panel) and Experiment 6 (lower panel). Key: ● S1, ◇ S2, × S3.

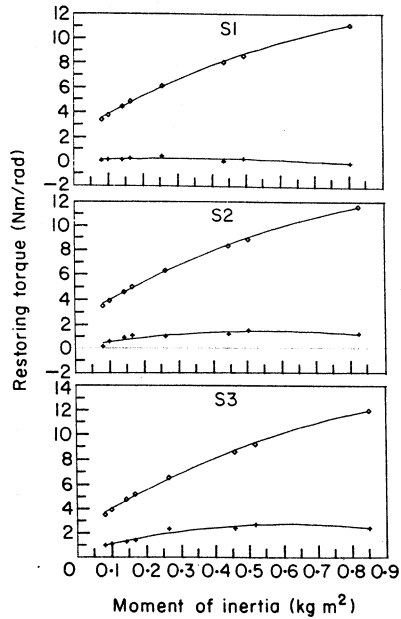


FIG. 22. Variation of  $G(\diamond)$  and  $K(+)$  as a function of moment of inertia for each of the three subjects in Experiment 5 (Subject 1, upper panel; Subject 2, middle panel; Subject 3, lower panel).

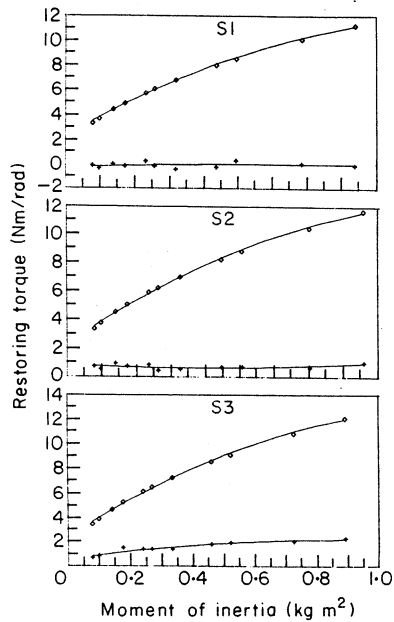


FIG. 23. Variation of  $G(\diamond)$  and  $K(+)$  as a function of moment of inertia for each of the three subjects in Experiment 6 (Subject 1, upper panel; Subject 2, middle panel; Subject 3, lower panel).

difference will be data points deviating from the ideal trajectories. Second, it has been noted that, for the individual human,  $K$  may relate to  $I$ . Under such conditions, equation (2) again predicts a nonlinear dependency of  $\tau_0^2$  on  $I$ , if  $K$  remains small relative to  $G$ , with the degree of curvature dependent upon the  $K$  to  $I$  mapping. The prediction is presented in Fig. 20.

Figure 21 presents the data from Experiments 5 and 6. In these experiments there was a wide range of  $I$  values and the relation of mass to length was constant (the conditions, therefore, are like those of the Sotavalta insect experiments). As can be seen, for each subject the relation of  $\tau_0^2$  to  $I$  was very reliable (all  $r^2$ s exceeded 0.99) and nonlinear. Also to be seen is the fact that the three subjects ordered the same way in the two experiments. This observation, in the context of Fig. 20 suggests that the subjects differed systematically in the relation to  $K$  to  $I$ —a conclusion that is buttressed by Figs 22 and 23. In those figures both the  $G$  and  $K$  quantities from the two experiments are plotted for each of the three subjects as a function of  $I$ .

### Time Allometries of Insects

Let us look further at the insect data. In Sotavalta's (1952, 1954) experiments, the relation between  $\tau_0^2$  and  $I$  was found to be linear, and  $K/4\pi^2$ , therefore, found to be constant, for each of the species studied. Consequently, given the differences among species in body size, Sotavalta (1952, 1954) was able to examine the relation of  $K$  to body size. We computed the regression of  $K$  on body mass. The quantities were derived from Table 1 of Greenewalt (1960) which reproduces Sotavalta's data. The linear regression ( $r^2 = 0.919$ ,  $P < 0.0001$ , 95% confidence limits, 0.999, 1.248) yielded the following power formula:

$$K(\text{Nm/rad}) = 0.838 \text{ body mass (kg)}^{1.124}. \quad (13)$$

We can use this fact to conduct a further evaluation of the appropriateness of equation (2) to the wing beat period of insects. In the manner of the analysis represented by Figs 5 and 6, we can inquire as to the behavior of  $M$  exp and  $L$  exp with variation in  $K$ .  $K$  has not been calculated in the manner detailed by Sotavalta for most of the many insect species on whom data have been compiled by Greenewalt (1962; Tables 1-6). Equation (13), however, permits an estimate of a given insect's  $K$  from the given insect's body mass, which is reported in the compilation. There are 131 insects in the data tabulated by Greenewalt (1962) for which the four measures of wing period, wing length, wing mass and body mass are given and 295 insects for which the three measures of wing period, wing length and body mass are given. By defining a small "window" of  $1.5 \times 10^{-5}$  kg in size and moving the leading edge of this window on the continuum of 131 body mass values in steps of  $1.5 \times 10^{-5}$  kg (starting at  $1.0 \times 10^{-5}$  kg), it is possible to embrace a number of insects (as few as five, as many as 13) of differing wing mass within each successive window. The data, parsed in the preceding manner, allowed a total of nine such windows. Taking the body mass value at a window's leading edge as the value representing the window, simple regression of log wing period on log wing mass gives the wing

mass-based time scale at each of nine body masses and, therefore, at each of 9  $K$  values given the power dependency of  $K$  on body mass.

A similar strategy can be brought to bear on the 295 insects for which wing period, wing length and body mass measures are available. The window size chosen was again  $1.5 \times 10^{-5}$  kg but—given the greater number of cases—the step size was reduced to  $0.5 \times 10^{-5}$  kg (starting at  $7.4 \times 10^{-5}$  kg). (The least number of cases within a window was seven, the largest number was 52.) The wing length-based time scale was computed for 35 successive values of body mass and, therefore, 35 successive values of  $K$ . The right panel of Fig. 24 presents the results of these computations; it reports the dependency of  $M \text{ exp}$  and  $L \text{ exp}$  on  $K$ , with  $K$  derived from the nine and the 35 body masses through the power formula above. The left panel of Fig. 24 presents the functional dependence of these exponents on  $K$  as follows from equation (2) constrained to the length scale of insects and with wing mass  $\propto$  wing length<sup>3</sup>. (For the insect data in Greenewalt (1962), the regression of wing mass on wing length is highly significant— $r^2 = 0.906$ ,  $P < 0.0001$ , for 142 degrees of freedom—with  $L \text{ exp}$  equal to 3.196 between 95% confidence limits of 3.025 and 3.361, and the intercept at 1 m equal to 0.992 kg.) The conclusion to be drawn from the comparison of the two panels of Fig. 24 is that the empirically determined insect time allometries are what would be expected if insect wing beat period was governed by the dynamical regime modeled by equation (2).

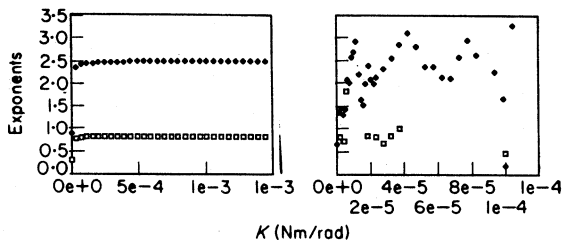


FIG 24. Dependence of time allometries on  $K$  for insects. Left panel presents the dependency of  $M \text{ exp}$  ( $\square$ ) and  $L \text{ exp}$  ( $\blacklozenge$ ) on  $K$  as follows from equation (2) tailored to the length scale of insects and with  $m \propto l^3$ . Right panel is based on insect data, using the relation  $K \text{ (Nm/rad)} = 0.838 \text{ body mass (kg)}^{1.124}$  to calculate  $K$  given body mass.

Using equation (2) a value of  $K$  can be computed for each insect given the measures of wing inertia (computed, after Weis-Fogh's (1973) suggestion, as  $ml^2/6$ ), wing mass, wing length and wing period. These computed  $K$  magnitudes should increase positively with body mass. The simple regression over logarithms confirms the expectation:  $r^2(130) = 0.891$ ,  $P < 0.0001$ , yielding the power formula  $K \text{ (Nm/rad)} = 0.991 \text{ body mass (kg)}^{1.201}$ . This power formula for  $K$  is in good agreement with that reported above based on Sotavalta's wing-clipping experiments (Greenewalt, 1960). (One outlier, the smallest insect in the 131 subset, was excluded from the computation—when this insect is included the coefficient is 1.53 and the exponent is 1.25.) A larger  $K$  means, of course, a shorter period. It is the case, however, that plotting wing periods against body masses yields a picture of periodic times lengthening as body mass increases. The  $r^2$  is small but reliable:  $r^2 = 0.124$ ,



$P < 0.0001$ , for the data set of 295 insects, and  $r^2 = 0.153$ ,  $P < 0.0001$ , for the subset of 131 insects. The exponent on body mass is 0.212 (with 95% limits of 0.148 and 0.277) and 0.244 (with 95% limits of 0.144 and 0.344) for the larger and smaller data sets, respectively; it is close to the range expected from the fundamental physiological time scales identified in the introduction. It is clear, however, that the time allometry  $\tau_0 \propto \text{body mass}^{0.212}$  or  $\text{body mass}^{0.244}$  is chimerical—it is the byproduct of doing a simple regression when a multiple regression is required.

Wing length and wing mass scale positively to body mass: wing length  $\propto$  body mass<sup>0.292</sup>,  $r^2(295) = 0.614$ ,  $P < 0.0001$  (95% limits of 0.266, 0.319; intercept at 1 kg, 0.220 m); wing mass  $\propto$  body mass<sup>1.142</sup>,  $r^2(131) = 0.740$ ,  $P < 0.0001$ , (95% limits of 1.024 and 1.259; intercept at 1 kg, 0.079 kg). From equations (2) and (11), and from considerations of the relation of  $K$  to body mass, we must expect that even though the two morphological variables are positively related, when wing period is regressed simultaneously on wing length and body mass the relation should be positive in the former case and negative in the latter case. A similar outcome is to be expected for the multiple regression of period on wing mass and body mass—a positive relation with wing mass and a negative relation with body mass. We can entertain another expectation. In these multiple regressions the inclusion of body mass (which ranges over four orders of magnitude from  $7.4 \times 10^{-7}$  kg to  $2.65 \times 10^{-3}$  kg) functions to homogenize  $K$  with respect to the regression of period on wing length and the regression of period on wing mass. Consequently, the exponents on these variables should comply with those observed in Fig. 24 and predicted from equation (2) for the length scale and mass-length relation of insects. For the multiple regression of  $\tau_0$  on wing length ( $WL$ ) and body mass ( $BM$ ):  $r^2(295) = 0.796$ ,  $P < 0.0001$ ,  $WL \text{ exp} = 2.137$ ,  $P = 0.0001$  (95% limits, 2.001 and 2.272),  $BM \text{ exp} = -0.412$ ,  $P = 0.0001$  (95% limits,  $-0.462$  and  $-0.361$ ). For the multiple regression of  $\tau_0$  on wing mass ( $WM$ ) and  $BM$ :  $r^2(131) = 0.884$ ,  $P < 0.0001$ ,  $WM \text{ exp} = 0.790$ ,  $P = 0.0001$  (95% limits, 0.736 and 0.845),  $BM \text{ exp} = -0.658$ ,  $P = 0.0001$  (95% limits,  $-0.731$  and  $-0.585$ ).

The expectations of how timing varies when just wing length or just wing mass is considered follow from equation (2) with negligible  $mlg$ . Given that wing mass is approximately proportional to body mass and  $K$  is approximately proportional to body mass,  $\tau_0^2 \propto BM \times l^2 / BM$ ; that is,  $\tau_0 \propto l$ . Simple regression on 342 insects from the Greenewalt (1962) compilation, those for which wing lengths and wing periods are provided, results in  $\tau_0 \propto$  wing length<sup>0.923</sup> ( $r^2 = 0.545$ ,  $P < 0.0001$ , 95% confidence limits on the exponent of 0.833 and 1.013; intercept at 1 m, 0.597 sec). Given that wing mass scales as wing length to approximately the 3 power, we would expect  $\tau_0$  to scale to wing mass close to the 1/3 power. Simple regression on the 142 insects for which the appropriate data are available yields  $\tau_0 \propto$  wing mass<sup>0.366</sup> ( $r^2 = 0.602$ ,  $P < 0.0001$ , 95% confidence limits on the exponent of 0.316, 0.415; intercept at 1 kg, 1.840 sec).

### The Relation of $K$ to Body Mass

As noted, insects and birds move their wings at an almost constant frequency, irrespective of flight maneuvers and speed of travel. In contrast, quadrupeds can

walk, trot and canter at a number of different frequencies. Within each gait, however, there is a preferred frequency which appears to be metabolically least costly (e.g. Hoyt & Taylor, 1981). Humans in the wrist-pendulum experiment can move similarly at many frequencies. However, under instructions to move rhythmically with maximum ease they exhibit, for any given load, a distinct preference (Kugler & Turvey, 1987). In pursuing the pendular, clocking mode as the dynamical regime underpinning these instances of absolute rhythmic co-ordination we are assuming that this co-ordination is conducted at the frequency that is most comfortable—always in the cases of insects and birds, usually in the case of quadrupeds, and readily in the case of humans. In short, it is assumed that the muscular driving force is in resonance—or very nearly so—with the characteristic frequency (or a characteristic frequency, as the case may be) of the free, undamped system comprising a wing or a limb and its related elastic elements.

Although vertebrates cannot duplicate the structure of the invertebrate elastic system (Weis-Fogh, 1973) they can approximate its function: vertebrate muscular tissue stores and uses mechanical energy when the mechanics of an activity demand that contracted muscles be stretched forcibly immediately before shortening—as would be the case in the oscillatory activity of wings and limbs relative to the body (Cavagna, 1977). This recovery of mechanical work is made possible by (a) the muscle's elastic elements (the tendons and the cross-bridges between actin and myosin) and (b) the disposition of the muscle's activated contractile machinery to resist lengthening forcibly enough to stretch the elastic elements (Cavagna, 1977; Huxley & Simmons, 1971; Rack & Westbury, 1974). Increasing the muscular force resisting lengthening increases the stretch of the elastic structures and the amount of mechanical energy that can be stored. The elastic restoring torque in oscillatory movements, therefore, is a quantity dependent on the number of active muscle fibers (Cavagna, 1977). According to Feldman's (e.g. 1986) lambda model, the tonic recruitment of fibers begins from a specific threshold length ( $\lambda$ ), with the recruitment and the resultant muscle force (to a first approximation) increasing as a function of the difference between the current muscle length and the threshold value. Again, it would seem that the mechanism for setting the  $K$  quantity for a given oscillatory movement resides in the neural components and processes that adjust  $\lambda$ . From the arguments and analysis presented here, quadrupeds and humans would seem to make systematic use of this mechanism.

Vertebrates and invertebrates obviously differ in the details of the system that provides elastic energy. We can ask, nonetheless, whether vertebrates share with invertebrates the same relation noted above between the elastic recoil (at the characteristic frequency) and body mass. The body mass relations for large birds reported above provide some hints to the answer. To reiterate, the multiple regression of wing period on body mass and wing length yielded a significant negative body mass exponent of  $-0.204$  ( $P=0.0001$ ) and a significant positive wing length exponent of  $0.961$  ( $P=0.0001$ ). Similarly, the multiple regression of wing period on body mass and wing mass yielded a significant negative body mass exponent of  $-0.517$  ( $P=0.0001$ ) and a significant positive wing mass exponent of  $0.587$  ( $P=0.0001$ ). By these multiple regressions, insects and large birds are similar in that the

bird wing-beat period is inversely related to body mass as would be the case if  $K$  is positively related to body mass. To determine the  $K$  values using equation (2), the wing moment of inertia for large birds was estimated in the same way as it was for the insects, namely,  $1/6(\text{wing mass} \times \text{wing length}^2)$ , and the length to the center of wing mass estimated as  $l/3$ . These are obviously very rough estimates of wing moment of inertia and location of wing center of mass given the complex transformation of a bird's wing during the cycle and the variability in bird wing design. At all events, the  $K$  values so derived, when regressed simultaneously ( $r^2 = 0.934$ ) on body mass, wing mass and wing length, relate significantly only to body mass ( $BM \exp = 0.672$ ,  $P < 0.03$ )—the one quantity not involved explicitly in  $K$ 's derivation.

The power formula relating  $K$  to the body mass of large birds,  $K \text{ (Nm/rad)} = 1.218 \text{ body mass (kg)}^{1.509}$  ( $r^2 = 0.896$ ,  $P < 0.0001$ ) approximates that for insects,  $K \text{ (Nm/rad)} = 0.838 \text{ body mass (kg)}^{1.124}$ . The corresponding power formulae for walking and cantering quadrupeds computed in like fashion also exhibit a similarity to the insect formula, at least with respect to the exponent:  $K \text{ (Nm/rad)} = 0.097 \text{ body mass (kg)}^{1.335}$  and  $K \text{ (Nm/rad)} = 0.158 \text{ body mass (kg)}^{1.238}$ , respectively. In Fig. 25,  $\log K$  is plotted against  $\log$  body mass for the insects, large birds and walking quadrupeds. For the quantities collected in Fig. 25,  $K \text{ (Nm/rad)} = 0.295 \text{ body mass (kg)}^{1.073}$ , ( $r^2 = 0.989$ ,  $P < 0.0001$ , 95% confidence limits 1.06, 1.11). One reading of Fig. 25 is that when an animal's center of mass is displaced by the cyclic movements of wings or limbs, the elastic energy per unit of body tissue at resonance frequency may be a constant, indifferent to the particular manner in which it is stored.

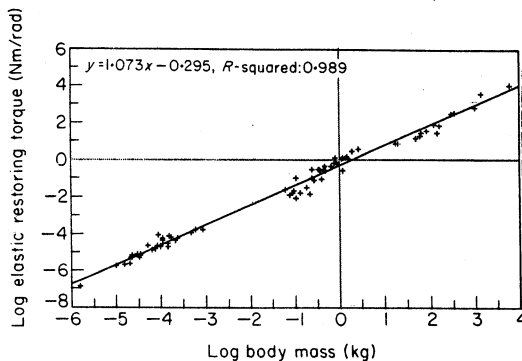


FIG. 25.  $\log K$  plotted against  $\log$  body mass for insects, large birds and walking quadrupeds.

### Conclusions

A long-standing problem in the allometric approach to biological laws is how to explain the empirically determined body-size relations (Calder, 1984; Peters, 1983). One prominent relation of this kind is the power formula that scales time as body mass to the  $1/4$  power—so-called physiological time. As noted at the outset of this paper, a very large number of physiological, developmental, and ecological cycles exhibit nearly parallel exponential relationships to body size (Lindstedt & Calder,

1981). Not all of these cycle times scale as closely to body mass<sup>1/4</sup> as might be desired, however, suggesting that it may be an oversimplification to express all physiological time allometries in terms of a single power formula (Calder, 1984).

The question can be raised of the constraints at work, universally, to produce this particular proportionality. One strategy for answering this question uses the tools of dimensional and similarity analyses. The strategy was depicted above in the generation of a time scale for wrist-pendulum systems. Here we state the strategy in more general terms. The typical physiological variable is usually expressed as a monomial in three dimensions—mass, length and time. If  $Y$  is a physiological variable then  $Y \propto M^a L^b T^c$ . It is possible to express  $Y$  in fewer dimensions if it is the case that there exists, for the systems under analysis, a fixed relation between any pair of dimensions. Suppose the systems are geometrically similar and of the same density. Geometric similarity means that volume ( $V$ )  $\propto L^3$ , and constant density means an invariant relation between mass and volume, namely,  $M = (\text{constant})V$ . Together, geometric similarity and constant density yield  $L \propto M^{1/3}$ . As a result,  $Y$  can be expressed as a monomial in just mass and time. If there is, in addition, a constant relating mass and time then the  $Y$  variable can be expressed as a power of a single dimension.

The preceding illustrates how constants constrain the relations among the fundamental dimensions. It can be supposed, therefore, that there is a particular set of biological constants that constrain the relations among time, mass and length to yield a physiological time scale proportional to body mass<sup>1/4</sup> and (representative) length<sup>1</sup>. In applying similarity analysis to biological systems, the strategy is to identify properties—invariant over differences in form and size—that explain the allometric exponents (e.g. Derome, 1977; Gunther, 1975). The strategy encounters two major problems. First, different constants or similarity criteria can generate different allometric relations. Consequently, the choice of constants must be guided by prior knowledge of the empirically determined exponent (Peters, 1983). Second, different constants or similarity criteria can generate the same allometric relation. The following are examples of biological constants that yield the scaling of physiological time to body mass<sup>1/4</sup> and to length<sup>1</sup>: the caloric constant and the weight density of animal tissue (Platt & Silvert, 1981); constant tissue elasticity, tissue tensile strength and tissue density (Economos, 1982); constant speed of propagation of electric impulses (Gunther, 1975; Lindstedt & Calder, 1981). Let us elaborate briefly on Platt & Silvert's (1981) analysis: the caloric content of tissue (J/kg) has dimensions of  $L^2 T^{-2}$ . Given that a constant in dimensional analysis is unity it follows that  $T \propto L$ . Similarly for weight density ( $N/m^3$ ), the dimensions are  $ML^{-2}T^{-2}$ , so  $L \propto M^{1/4}$  and  $T \propto M^{1/4}$ .

In brief, there are not enough constraints on the methods of dimensional analysis and similarity analysis to provide a principled understanding of the physiological time scale and, perhaps, of empirically determined biological scaling relations more generally (Derome, 1977; Iberall, 1979; Peters, 1983; Prothero, 1986). In this article we have focused on the co-ordination that characterizes most forms of mammalian, avian and insect locomotion, namely, absolute co-ordination (von Holst, 1939/1973) in which two or more limbs or wings oscillate together at a fixed phase relation, at

a single common tempo, and with the minimum possible of muscular energy. Our contention is that the time scales observed for this co-ordinated rhythmic activity are the consequences of the physics that underwrites this activity. They do not derive from any constants of biological tissue. Absolute co-ordination can be expressed physically as a single, dynamical regime in which a point mass  $m$  on a massless, rigid rod of length  $l$  oscillates about a fixed point under two conservative restorative forces—one due to gravity and one due to a spring (which is provided, for biological instances of this regime, by tissues of the body). An observed periodic time in absolute co-ordination performed comfortably will be close to the characteristic or resonant period of a hybrid mass-spring/simple pendulum system (see Fig. 1) that is free and undamped: as observed in equation (2),  $\tau_0 = 2\pi[ml^2/(mgl + kb^2)]^{1/2}$ . We conclude our examination of the richness of this simple equation by noting the nature of the relations it defines in the space of log periodic time  $\times$  log length, and the space of log periodic time  $\times$  log (limb or wing) mass, over the range of lengths spanning the smallest insect and the largest mammal.

We wish to confine equation (2) to biology. And we wish to make the confinement as general as possible, in order to expose the most general relationships. To do this we apply two restrictions: (1)  $m \propto l^3$ , that is, the mass of the pendulum is proportional to the cube of its length, and (2)  $kb^2 \propto m^1$ , that is, the restoring torque due to the spring is proportional to the pendulum's mass. The bulk of the available evidence shows that biological systems are more nearly geometrically similar than anything else (Peters, 1983). With respect to a specific pendular component, wing mass scales to wing length to the third power. This is certainly not perfectly true for all species (see, for example, Warham, 1977) but it is the most representative scaling, applying quite generally to the roster of flying animals, including perhaps the hummingbirds (see Greenewalt, 1962, Fig. 9). On the basis of Figure 25, the elastic restoring torque in wing or limb oscillations at characteristic period is directly proportional to body mass. (Relatedly, Gunther & Leon de la Barra (1966) note that aortic elasticity and lung and thoracic compliance in mammals scale as body mass to the 1.19 power and 1.04 power, respectively; and Stahl (1967) notes that lung compliance in mammals scales as body mass to the 1.08 power.) In the system described by equation (2) and depicted in Fig. 1, there is no component analogous to body mass; the only mass is that of the pendulum. Although it is the only option, letting elastic energy scale as pendulum mass  $m$  is not unsound biologically. The masses of biological pendular components—wings and limbs—tend to scale to body mass to the first power. The elastic restoring torque should scale, in the ideal, therefore, close to the first power of the mass of the wing or limb pendulum.

The upper panel of Fig. 26 shows the relation between log period and log length for equation (2) under the above restrictions (1) and (2), and over the range of lengths covering flying insects and quadrupeds. The relation is significantly quadratic ( $P < 0.0001$ ) and linear ( $P < 0.0001$ ). The middle and lower panels of Fig. 26 show the relation between the two variables for the ranges of length  $< 0.1$  m and length  $> 0.1$  m, respectively. In both panels the relations are highly linear with significant quadratic components. Across the two panels, however, the slopes of the linear regression lines differ markedly: for the length  $< 0.1$  m range the slope approximates

(Lindstedt & Calder, 1981) may be understood as the result of that physics when it is observed over the length range of 0.003–10 m, or a good portion of it. More restricted ranges, however, would lead to observed departures from the mass<sup>1/4</sup> allometry. Inspection of the allometric functions compiled by Calder (1984) and Peters (1983) reveals that such departures do occur, and the middle and lower panels of Fig. 27 show how they could arise by truncating the length range over which equation (2) operates.

Finally, we note that the locomotion time scales can be expressed in terms of (a) limb or wing mass, (b) limb or wing length, and (c) body mass. With respect to equation (2), variables (a) and (b) compose the inertia term in the numerator and the gravitational restoring term in the denominator. Variables (a) and (b) relate positively to variable (c). Variable (c)'s contribution, however, appears to be limited to the elastic restoring term in the denominator. The technique of multiple regression is required to reveal this pattern of dependencies of periodic time on the magnitudes of limb or wing and of body. Expressing time in terms of body mass—the result of simple regression—may not be illuminating, in itself and in the absence of a suitable physical theory that demonstrates the intrinsic relationship among all of the necessary variables.

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#### REFERENCES

- ADOLPH, E. F. (1949). *Science, N.Y.* **109**, 579.
- BUCHTAL, F. & WEIS-FOGH, T. (1956). *Acta physiol. scand.* **35**, 345.
- CALDER, W. A. III (1984). *Size, Function and Life History*. Cambridge, MA: Harvard University Press.
- CAVAGNA, G. (1977). *Exercise Sports Sci. Rev.* **5**, 89.
- DEROME, J. R. (1977). *J. theor. Biol.* **65**, 369.
- ECONOMOS, A. C. (1982). *J. theor. Biol.* **94**, 25.
- FELDMAN, A. G. (1966a). *Biophysics* **11**, 565.
- FELDMAN, A. G. (1966b). *Biophysics* **11**, 766.
- FELDMAN, A. G. (1974). *Biophysics* **19**, 544.
- FELDMAN, A. G. (1980). *Neuroscience* **5**, 81.
- FELDMAN, A. G. (1986). *J. Motor Behav.* **18**, 17.
- GARLAND, T. (1983). *J. Zool, Lond.* **199**, 157.
- GREENEWALT, C. H. (1960). *Proc. Am. phil. Soc.* **104**, 605.
- GREENEWALT, C. H. (1962). *Smithson. Miscell. Collect.* **144**, 1.
- GREENEWALT, C. H. (1975). *Trans. Am. phil. Soc.* **65**, 1.
- GUNTHER, B. (1975). *Physiol. Rev.* **55**, 659.
- GUNTHER, B. & LEON DE LA BARA, B. (1966). *Acta physiol. Lat. Am.* **16**, 32.
- GUNTHER, B. & MORGADO, E. (1982). *J. theor. Biol.* **96**, 543.
- HILL, A. V. (1950). *Sci. Prog.* **38**, 209.
- HOYT, D. F. & TAYLOR, C. R. (1981). *Nature, Lond.* **292**, 239.
- HUXLEY, A. F. & SIMMONS, R. M. (1971). *Nature, Lond.* **233**, 533.
- IBERALL, A. S. (1979). *Am. J. Physiol.* **237**, R7.
- KUGLER, P. N. & TURVEY, M. T. (1987). *Information, Natural Law and the Self-assembly of Rhythmic Movement*. Hillsdale: Erlbaum.
- LINDSTEDT, S. L. & CALDER, W. A. (1981). *Q. Rev. Biol.* **56**, 1.
- MCMAHON, T. A. (1975). *J. appl. Physiol.* **39**, 619.

- MCMAHON, T. A. (1980). *Lectures Math. Life Sci.* **12**, 131.
- MCMAHON, T. A. (1984). *Muscles, Reflexes and Locomotion*. Princeton: Princeton University Press.
- MAGNAN, A. (1922). *Ann. Sci. nat.* **5**, 125.
- MEINERTZHAGEN, r. (1955). *Ibis* **97**, 111.
- PEDHAZUR, E. (1982). *Multiple Regression in Behavioral Analysis*. New York: Holt, Rinehart & Winston.
- PENNYCUICK, C. J. (1968). *J. exp. Biol.* **49**, 527.
- PENNYCUICK, C. J. (1975). *J. exp. Biol.* **63**, 775.
- PETERS, H. P. (1983). *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.
- PLATT, T. & SILVERT, W. (1981). *J. theor. Biol.*, **93**, 855.
- PROTHERO, J. (1986). *J. theor. Biol.* **118**, 259.
- RACK, P. M. H. & WESTBURY, D. R. (1974). *J. Physiol., Lond.* **240**, 331.
- RAYNER, J. M. V. (1979). *J. exp. Biol.* **80**, 17.
- SOTAVALTA, O. (1952). *Ann. zool. Soc. "Vanamo"* **15**, 1.
- SOTAVALTA, O. (1954). *Ann. ent. fenn.* **20**, 93.
- STAHL, W. R. (1962). *Science, N.Y.* **137**, 205.
- STAHL, W. R. (1967). *J. appl. Physiol.* **22**, 453.
- TUCKER, V. A. (1972). *Am. J. Physiol.* **222**, 237.
- TURVEY, M. T., ROSENBLUM, L. D., SCHMIDT, R. C. & KUGLER, P. N. (1986). *J. exp. Psychol. Human Percep. Perform.* **12**, 564.
- VON HOLST, E. (1935/1973). *The Behavioral Physiology of Animal and Man*. Coral Gables: University of Miami Press.
- WEIS-FOGH, T. (1973). *J. exp. Biol.* **59**, 169.