Scaling of the Locomotory Apparatus and Paddling Rhythm in Swimming Mallard Ducklings (*Anas platyrhynchos*): Test of a Resonance Model

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ABSTRACT It was hypothesized that the constant propulsive frequencies observed in several paddling animals as they swim at different speeds reflects "resonance-like" swimming mechanics. This behavior may result if the hydrodynamic load on the paddle is dominated by acceleration-dependent, rather than velocity-dependent, terms, and the musculoskeletal system operates with nearly constant stiffness over a large fraction of the propulsive cycle. A model was developed that uses the form of the paddle and the architecture of a representative limb muscle (lateral gastrocnemius) to predict a value proportional to propulsive frequency in mallard ducklings of different size. Fifteen ducklings were videotaped as they swam in a water channel, and the measured frequencies were compared to model predictions. Although the predicted and measured frequencies were highly correlated ($r = 0.926$), the **95%** confidence interval estimated for the intercept of the reduced major axis fit to the points did not span the origin. This lack of proportionality means that even though it could account for much of the observed variation in paddling frequencies, the present model of resonance-like swimming is not supported. © 1994 Wiley-Liss, Inc.

The propulsive mechanisms used by fish and secondarily aquatic animals may be divided into three modes according to the means by which thrust is produced: lift-based, inertia-based, and drag-based (Daniel and Webb, '87). Each of these modes is characterized by a set of constraints on the morphology and behavior of the animals that use them. The present report describes an attempt to relate morphology to a feature of swimming behavior seen in one of these groups, the drag-based, or paddling swimmers.

Lift-based and inertia-based swimmers swim faster in part by increasing the frequency of their propulsive movements (see Webb, '86, for earlier references). In contrast, several drag-based swimmers (although not all; see Discussion) use a single propulsive frequency that does not vary with swimming speed. Constant frequencies have been reported by Prange and Schmidt-Nielsen ('70) for mallard ducks, Nadel ('77) for human competition swimmers, Williams (**'83**) for mink, Fish ('84) for muskrats, and Williams ('89) for sea otters. The use of constant frequencies in independently evolved, drag-based swimmers suggests a common underlying mechanism for that swimming mode.

At least three distinct mechanisms have been described that could dictate the frequency of oscillation of an appendage: (1) The frequency is set by an independent pattern generator in the central nervous system (Delycom, '80). (2) The frequency is defined by fixed latencies of nervous transmission, which lead to a dominant frequency of reflex-loop instability. (3) The frequency is determined by a mechanical resonance (see, e.g., Stein and Lee, '81). For drag-based swimming animals, only Prange and Schmidt-Nielsen ('70) suggested any cause for constant frequencies; they proposed that the third mechanism, mechanical resonance, might be responsible, although they offered no experimental evidence for it.

Mechanical resonance involves the cyclic exchange of energy between two forms, such as elastic potential and kinetic energies (Den Hartog, '85). For large-amplitude resonance of a submerged vertebrate appendage, there would have to exist appropriate "masses" and "springs" to contain the cycling energy, and the losses of energy due to friction would have to be relatively modest (subcritical damping). As outlined below, the force of water against the moving paddle may behave like a mass, and the combination of a limb's

muscles, tendons, and segmental reflexes may act as an appropriate spring. In the proposed scheme neither of these elements may actually be capable of both storing energy and later returning it to the system. We hypothesize that a single frequency might nevertheless characterize cyclic movements of the paddle, provided the mass is nearly constant and the spring is nearly linear over a large enough fraction of the motion, We refer to this mechanism as "resonance-like."

Mass-like loading of the propulsive organs is increasingly being recognized as an important factor in the mechanics of aquatic locomotion (Daniel, '84; Daniel and Webb, '87). The forces exerted on a propulsor in the direction it moves through the water may be decomposed into drag, which is a function of relative velocity, and an acceleration reaction, which depends on the acceleration and deceleration of the organ as it executes its periodic swimming motions. Recent estimates (e.g., Blake, '79, '86; Daniel, '85) indicate that the acceleration reaction may be the predominant force in some swimmers. If this is true for paddling animals, the "added mass" of accelerated water might interact with the stiffness of the propulsor to yield a mechanical resonance. This type of argument has been offered by DeMont and Gosline ('88) to explain the mechanics of propulsion in the jellyfish, *Polyorchis,* but to our knowledge it has not been applied previously to vertebrate swimmers.

The concept of spring-like behavior of the musculoskeletal systems of vertebrates has received much recent attention. The elastic behavior of ensembles of muscles and tendons during terrestrial locomotion appears to enhance mechanical efficiency in many animals (Cavagna et al., '88; R. McN. Alexander, '88). In addition, it has been suggested that the linearizing effect of segmental reflexes on muscle mechanics may simplify computational problems in motor control (Nichols and Houk, '76; Houk, '79). Several authors (e.g., Blickhan, '89; Farley et al., '91, '93; Greene and McMahon, '79; McMahon, '85; McMahon and Greene, '79; MacMahon et al., '87; McMahon and Cheng, '90; Taylor, '85) have modeled the mechanics of the limbs of running animals and humans with single springs that reflect the composite behavior of all of the limbs' tendons, muscles, and reflexes.

The present investigation into limb stiffness and dynamic loads during paddling ties in with a substantial body of work relating musculoskeletal proportions to performance across animals of different size (Hill, '50; see, e.g., Pedley, '77; Turvey et al.,

'88). In contrast to many of these efforts, the present study was not motivated by a desire to determine the rules governing relative growth or the exponents of physiological scaling across species of different size. Rather, like the study of McMahon ('75), variations that occur with body size were used as a tool to investigate the plausibility of a particular mechanism. However, the present model employs the same basic premise as McMahon's ('73, '75) model for elastic similarity of animals of different size: stiffness should be matched to the load of a mass. In McMahon's formulation, the load is the force required to support the mass of the body against gravity, whereas in the present model, the relevant load is the force required to accelerate the "added mass" of water during a propulsive stroke.

The hypothesis of resonance-like swimming was evaluated by devising a model based on musculoskeletal features, and comparing the model's predictions with measured paddling frequencies.. Because the resonance model only predicts a value proportional to frequency, it was only possible to test it by determining whether the ratio of predicted to measured frequencies was constant across a range of model inputs. This range was established with an ontogenetic series of mallard ducklings, for which the paddling frequencies and relevant morphological parameters both change with age. Although not the primary aim of the study, the data permitted comparisons between duckling morphology and the predictions of the well-known geometric, elastic, and static stress models of scaling (McMahon, '75). Thus these models provide a range of alternative hypotheses to resonance-like paddling.

THE RESONANCE MODEL

The model is based on a simple mechanical resonance of a mass-like hydrodynamic load on a spring-like musculoskeletal system. The resonant frequency (f, in Hz) of such a system is given by (Den Hartog, '85):

$$f = (K_l/M_v)^{0.5}/2\pi \qquad (1)$$

where K_l = the stiffness of the entire hind limb, and M_v = the virtual mass of the foot, i.e., the sum of foot mass and the "added mass" of water acting on it (Blake, '79) during the propulsive phase of the paddling cycle. The frequency f is taken to mean the frequency that would be exhibited by a paddle that moved symmetrically backward and forward. In a paddling duckling,

however, the propulsive and recovery phases are not equivalent; the webbed foot is folded during the recovery phase, and thus its added mass is reduced, compared to the propulsive phase. Strictly speaking, the frequency described by equation 1 only applies to the propulsive phase. However, the duration of the propulsive phase is a constant fraction of the duration of the entire cycle, i.e., the duty factor is constant, in ducklings of different sizes (Fish, unpublished observations). Therefore, it has been assumed that f is proportional to the frequency of paddling. In addition, damping was ignored; constant, subcritical damping should lower the frequency of resonance by a fixed proportion (Den Hartog, '85), but this would not affect the test described below.

While estimation of M_v is straightforward (see below), K_l could not be evaluated directly, as it should be set by the level and pattern of muscular recruitment during swimming, as well as by the gating of various proprioceptive reflexes. However, by making a series of assumptions, it was possible to arrive at a measure that is proportional to K_l, as follows. First, it was assumed that for all ducklings, stiffness of the entire limb is proportional to the stiffness of just one of the muscles used in swimming. The lateral head of the gastrocnemius was selected for this purpose, based on its anatomical position, which makes it likely involved in the power stroke of the paddling cycle. The stiffness of this muscle during swimming is designated K_g, thus

$$K_l \propto K_g. \qquad (2)$$

Although K_g could be measured directly in situ (e.g., Hoffer et al., '89), the present study takes an approach that is much simpler technically, although it requires more assumptions. This approach utilizes the concept of "normalized stiffness" introduced by Houk and Rymer ('81). These authors propose that the ratio of a muscle's range of force output to its range of deformation (i.e., a stiffness) might be reasonable for certain comparisons across muscles and species. As a first approximation the stiffness of the lateral gastrocnemius during paddling might be fixed across individuals at some constant fraction of the normalized stiffness, defined as the ratio of the muscle's maximum isometric force (P_0) to the difference between resting length (L_0) and the length at which the muscle can no longer generate force (L_{min}). Thus, adding the letter g to the subscripts to denote the gastrocnemius,

$$K_g \propto P_{0g}/(L_{0g} - L_{min,g}). \qquad (3)$$

Finally two assumptions are applied which are common in descriptions of vertebrate muscle (Close, '72). First, following Hill ('50) the maximum isometric force a muscle can produce is assumed to be proportional to physiological cross-sectional area, irrespective of the speed of contraction or type-composition of the muscle's fibers. Although there have been some contradictory findings on this point, the most recent measures (Bodine et al., '87; Lucas et al., '87; Chamberlain and Lewis, '89), indicate little, if any variation in "specific tension" (maximum isometric force/cross-sectional area) among mammalian motor unit types. Here the assumption is made that specific tension is constant within a single muscle in an ontogenetic series of ducklings, and thus that P_{0g} is proportional to the cross-sectional area (CSA) of the lateral gastrocnemius, which may be estimated by the ratio of muscle mass to the average resting length of the muscle fibers:

$$P_{0g} \propto CSA \propto M_g/L_{0g}. \qquad (4)$$

The second assumption is that muscle fibers may shorten by a fixed fraction of their resting length:

$$(L_{0g} - L_{min,g}) \propto L_{0g}. \qquad (5)$$

Finally, substitution of (4) and (5) into (3), then (3) into (2), and (2) into (1), and combining the 2π with all the other constants of proportionality into a single constant C, gives:

$$f_p = C \times (M_g/(M_v \times L_0^2))^{0.5} \qquad (6)$$

where f_p denotes predicted frequency.

Thus, this model of resonance-like behavior of the propulsive system predicts that the frequency used by a duckling should be proportional to a simple combination of measurements of foot virtual mass and the mass and fiber length of the gastrocnemius. If the model is correct, then for a sample of animals that paddle at different characteristic frequencies, the relationship between measured (f_m) and predicted (f_p) frequencies will appear as a linear one passing through the origin.

METHODS

Experimental animals

Fifteen newly hatched mallard ducklings (*Anas platyrhynchos*) were obtained from a commercial

dealer. They were maintained indoors in a 2 *x 2* m enclosure on a 12:12 light:dark cycle at 21°C, and fed commercial duck feed. **A** circular artifi-**cial** pond 1.2 m in diameter and 0.25 m deep was placed in the enclosure to allow the animals to swim freely Although they were not trained or compelled to swim prior to the day of experimentation, the ducklings were often observed swimming spontaneously. The ducklings were arbitrarily divided into three groups of five, which were used for experiments **1**,14, and **28** days after acquisition.

Water channel

Measurements of swimming speed and paddling frequency were made while the ducklings swam in a recirculating water channel that is based on the design of Vogel and LaBarbera ('78). The working section of the channel was 0.29 m wide and 0.19 m deep. The upstream end of the working section was bounded by a 0.025 m square plastic grid to reduce turbulence. Water in the channel was circulated by a Mercury electric outboard motor (Model 10019) mounted with its propellor in the return channel below the working section. The motor was powered by a 12 V storage battery connected to a 6 **A** battery charger. Water speed in the channel was determined for each run by timing the movement of drops of india ink added to the upstream end of the working section.

Paddling frequencies

Ducklings were videotaped (Panasonic PV200D camcorder) through the Plexiglas wall of the channel as they swam at different speeds. Every specimen in a particular group was measured at a given channel speed for roughly **30** sec, then removed and rested for several minutes before the next trial. The younger ducklings could not hold their positions in the flume at high water speeds for more than a few seconds; although the top speeds attainable by each size class were not sought systematically, every specimen in the group was able to swim steadily for at least 30 sec at speeds up to 30 cm/sec for the 1-day ducklings, up to 56 cm/sec for the 14-day ducklings, and up to 66 cm/sec for the 28-day ducklings. For each trial a swimming sequence was selected for analysis in which the duckling stayed in the center of the channel, did not accelerate or decelerate in the channel flow, and paddled continuously for 10 or more strokes with both feet. The number of videotape fields (30 fields/sec) required to perform 10 complete cycles (beginning of the first power

stroke to end of the tenth recovery stroke) of the left foot was measured using a Panasonic AG-6300 videotape recorder, and the result converted to paddling frequency. For each specimen the mean of the frequencies (f_m) measured at various flume speeds (except as noted below) was used for comparisons to the model.

Virtual mass of the foot

Immediately after videotaping, the feet of each duckling were photocopied to obtain foot planiforms for estimation of virtual mass. Care was taken that the foot webbing was fully spread. Planiforms were assumed to be representative of a fully spread foot during paddling.

The virtual mass represents the fluid accelerated by a body in unsteady motion (Webb, '75; Blake, '79). The virtual mass of the duckling foot was calculated according to the blade-element analysis used by Blake ('79). Blade-elements were arranged at 0.2 cm intervals (Δl) perpendicular to the median long axis of the foot. The virtual mass of the ith element (m_i) is given by the equation:

$$m_i = \pi \times (c_i/2) \times \Delta l \times \rho$$

where c_i is the chord (distance perpendicular to the long axis) of the foot at the midpoint of element i, and ρ is the density of water. The virtual mass of the entire foot (M_v) was calculated by summing m_i over the length of the foot.

Morphometry of the gastrocnemius

The ducklings were killed by placing them in a closed container saturated with chloroform vapors. Subsequently they were removed and preserved by immersion in 10% formalin in avian Ringer's solution (Wilson, '72). For preservation, the knee and ankle joints were both set to 40" (characteristic angles for the start of the propulsive stroke at moderate swimming speeds) **by** visual inspection and palpation, and secured with thread and small nails to wooden boards. After 1–2 weeks of preservation the left lateral gastrocnemius muscle was carefully dissected from each duckling, trimmed of excess connective tissue and external tendons, blotted, and weighed to the nearest mg. The mass of each muscle was taken as the mean of three estimates.

An estimate of the average length of muscle fibers was made by assuming that fibers run the entire length of the muscular fascicles. While there is growing evidence that this is not correct for

many avian muscles, for the purposes of the model it is only important that on average, fibers extend a fixed fraction of the length of the fascicles (see Discussion), for in that case the difference is encompassed in the constant of proportionality C **of** equation **6.** Fascicle lengths were determined by nitric acid digestion, as described by Maxwell et al. ('74). Each muscle was placed in a shallow dish of 30% HNO_3 for 5–7 days. When the fascicles were clearly separable the acid was replaced with 50% glycerol. The muscle was then divided parallel to its fibers into 16 roughly equal parts, and from each part an intact fascicle was teased free. Fascicle length was measured to the nearest 50 μm using a dissecting microscope equipped with an ocular micrometer. For each animal the gastrocnemius fiber length L_0 was taken as the mean of the **16** fascicle lengths.

Statistical analyses

Both linear regressions and reduced major axes (model II regression; Sokal and Rohlf, '81) were fitted to the logarithmically transformed data in order to assess their agreement with the various scaling models. Residuals were inspected visually to assess the adequacy of the fits. Ninety-five percent confidence intervals for the slopes of the reduced major axes were computed using the method of Rayner (**'85).** In addition, to avoid the assumption of bivariate normality, percentile confidence intervals were estimated from the distribution of 1,000 bootstrap iterates (Efron and Tibshirani, '86), as proposed by Plotnick ('89).

If it is correct, the resonance model (equation 6) yields a number (f_p) proportional to the measured swimming frequency (f_m), with the constant of proportionality representing a consolidation of the various constants discussed above. The model may be tested by determining whether the relationship between f_p and f_m can be described by a straight line of finite, non-zero slope passing through the origin. The slope and intercept of the reduced major axis fit to the data were used for this test. Confidence intervals for the slope were estimated as described for the morphometric measurements. Confidence intervals for the intercept of the relationship were estimated from both the formula for standard error given by Imbrie ('56) as well as from the distribution of 1,000 bootstrapped samples (Plotnick, '89).

RESULTS

All ducklings paddled at frequencies that remained roughly constant over a range of swimming speeds (Fig. 1).Several members of the 14- and 28-day-old groups, however, could not be induced to paddle continuously at the slowest flume speed tested (25 cm/sec). Instead, they interspersed periods of backwards drifting with bouts of relatively vigorous paddling to regain position in the flume; the average paddling frequencies during these bouts were roughly 20–30% greater than those for steady swimming for all 10 specimens. Thus the frequencies of paddling for ducklings in the 14- and 28-day groups at 25 cm/sec were not included in subsequent calculations. The average measured paddling frequency (f_m) tended to decline with increasing body mass (Fig. 2).

Masses, fiber lengths, and cross-sectional areas of the lateral gastrocnemius, as well as the estimated virtual mass of a paddling foot for each duckling are shown as a function of body mass in Figure 3a–d. Slopes of both linear regressions and reduced major axes of the logarithmically transformed data from Figures 2, 3b,c are listed in Table 1. The slopes of the reduced major axes are consistent with McMahon's ('73, '75) model of elastic similarity: paddling frequency scales as $mass^{-0.126}$ (prediction $= -1/8 = -0.125$); muscle fiber length scales as $mass^{0.269}$ (model prediction $= 1/4 = 0.25$); and muscle CSA scales as $mass^{0.774}$ (prediction $= 3/4 = 0.75$). The linear regression slopes are not very different, in accord with the high values of the correlation coefficients. The various estimates of 95% confidence intervals for the slopes of these relationships all include the predicted values for elastic similarity. The pre-
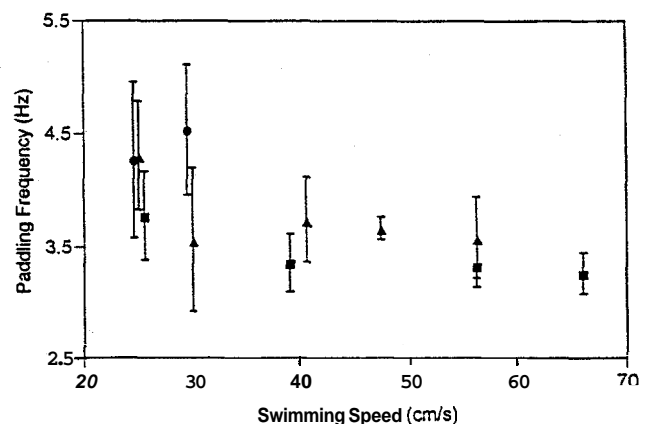

Fig. 1. Paddling frequency vs. swimming speed in three age classes of ducklings. Error bars denote ± 1 standard deviation; n = **5** in all groups. Solid circles: **1** day old; solid triangles: **14** days old; solid squares: **28** days old.
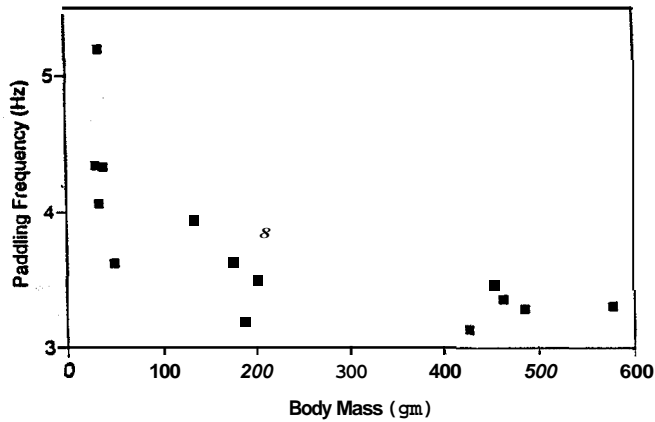
Fig. 2.　Mean paddling frequency vs. body mass.

dicted values under the geometric and static stress models for slopes of fiber length, muscle CSA, and paddling frequency (see McMahon, '75) all fall outside all of the estimated 95% confidence intervals, except for the slope of muscle CSA under the static stress model (4/5 = 0.80).

Figure 4 shows the relationship between pre-

dicted and measured paddling frequency for each duckling. The two measures are highly correlated ($r = 0.926$; $P < 0.001$). The fitted line denotes the reduced major axis (slope = 0.049; y-intercept = −0.067). The 95% confidence intervals for slope and intercept computed by different techniques are listed in Table 2. The residuals from neither the reduced major axis nor the linear regression (slope = 0.046; y-intercept = -0.053) showed any visually detected trend; either of these straight line fits appears to represent the data adequately.

The confidence intervals for the y-axis listed in Table 2 do not span the origin, although they fall just outside it. A regression line forced through the origin (slope = 0.0317) is not an adequate fit; predicted values are too low at low frequencies and too high at high frequencies. Thus, the model predicts values that are not proportional to measured frequencies; an additional offset is required.

DISCUSSION

Because the estimates of the confidence interval for the y-intercept of the functional relationship between predicted and measured frequencies
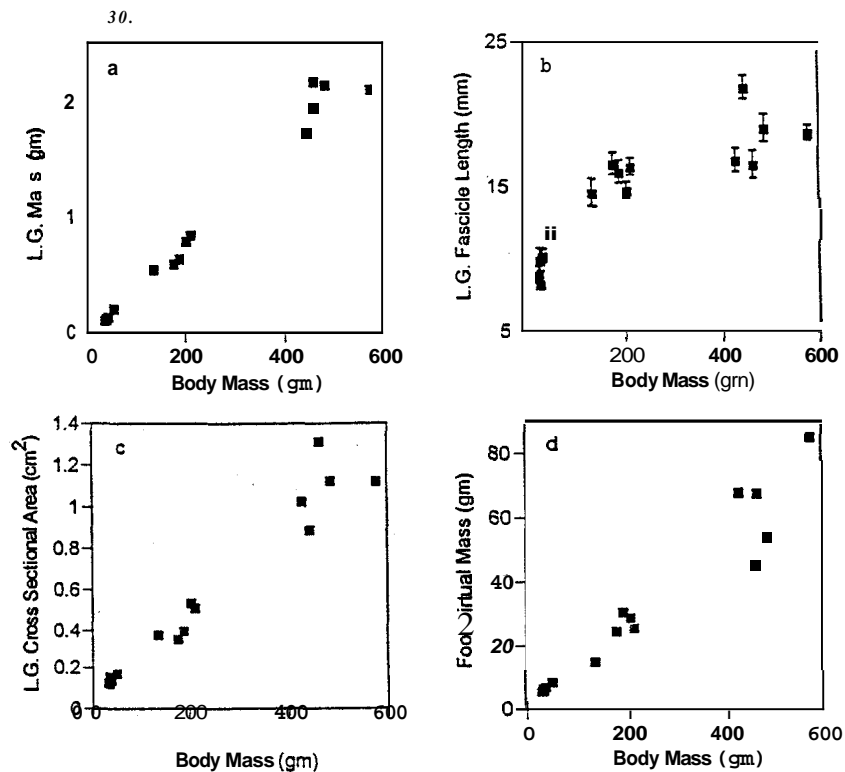

Fig. 3.　Morphological characters of the paddling apparatus, all plotted against body mass. a: Mass of the lateral gastrocnemius. b: Length of fibers of the lateral gastrocnemius (mean ± 1 standard deviation; n = 16). c Estimated cross-sectional area of the lateral gastrocnemius. d Estimated virtual mass of a single foot during the propulsive stroke.

TABLE 1. Linear regression and reduced major axis slopes and 95% confidence intervals for logarithmically transformed morphometric data and paddling frequency against body mass

	L_0 vs. M_b	CSA vs. M_b	M_v vs. M_b	F_m vs. M_b
Linear regression slope	0.254	0.764	0.859	−0.104
95% C.I.	0.203–0.306	0.689–0.839	0.780–0.937	−0.147– −0.062
RMA slope	0.269	0.774	0.869	−0.126
95% C.I.				
Rayner (1985)	0.219–0.330	0.701–0.855	0.792–0.953	−0.176– −0.091
Bootstrapped	0.216–0.316	0.710–0.844	0.799–0.937	−0.170– −0.085
Correlation coefficient(r)	0.947	0.987	0.988	0.825

do not span the origin, the resonance model is not supported. This result may be interpreted as indicating that the mechanical interactions between the duck's paddle and the water do not operate in a "resonance-like" mode, and that some other mechanism must be responsible for the constancy of paddling frequency in this species. Given the near-perfect agreement between the data and the predictions of elastic similarity, it seems reasonable to suggest that the determinants of fiber length and CSA of the lateral gastrocnemius are similar to those of other systems that obey this scaling behavior, and are not dominated by the dynamics of the paddling foot.

Alternatively, various size-dependent errors in the morphometric measurements, e.g., systematically overestimating the virtual mass of the foot in small specimens, could have biased the relationship toward the observed one. Several assumptions, e.g., of muscles being activated to a constant

fraction of their possible maximum, or straining by a constant fraction of fiber length, may not hold across the range of body size. It was observed that the architecture of the fiber bundles in the lateral gastrocnemius became slightly more complicated with age; in older specimens, fibers more obviously converged on a central tendon of insertion. Thus a size-dependent bias in physiological cross-section may have been incorporated into the data. (Because fiber pinnation angles were estimated to be low, this feature was not incorporated into the original model.)

A further potential problem in the estimation of predicted frequency could arise if the ratio of muscle fiber length to fascicle length varies with duckling size. Although there are no data that address this issue for the lateral gastrocnemius of ducks, Gaunt and Gans ('90) report that muscle fibers grow in proportion to the length of the whole muscle in various hind limb muscles of the chick, based on spacing between bands of motor endplates. If this is not also the case for ducklings, a size-dependent bias in the estimates of fiber length would affect the estimates of both CSA (equation 4) and muscular shortening (equation 5), and thereby strongly bias f_p (equation 6).

In addition to potential problems with the assumptions about muscular architecture, it is likely to be oversimplistic to assume that the duck's hind limb is shaped only by the requirements for thrust
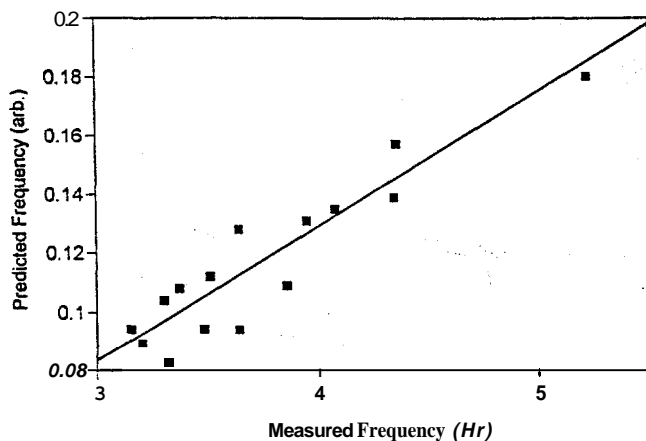

Fig. 4. Predicted frequency vs. measured paddling frequency. Predicted frequency (f_p; see text) was computed according to equation 6 for each duckling. The fitted line represents the reduced major axis: $f_p = -0.0668 + (0.0491 \times f_m)$.

TABLE 2. Reduced major axis slope and intercept values and confidence intervals for predicted vs. measured paddling frequency

	Slope	Intercept
RMA value	0.0491	−0.0668
95% C.I		
Rayner (1985)	0.0383–0.0630	
Imbrie (1956)		−0.106– −0.028
Bootstrapped	0.0426–0.0642	−0.122– −0.040

production or for swimming alone. The paddling stroke is divided into a power phase for thrust production and a recovery phase to reposition the limb for the next stroke (Blake, '79, '80; Fish, '84). These phases are not symmetrical; the webbing of the foot is fully spread to accelerate a large mass of water posteriorly during the power phase, whereas it is folded during the recovery phase to reduce fluid forces. The morphology of the foot and limb must be adequate for the requirements of both phases. Furthermore, in terrestrial locomotion, the limbs must support and propel the animal's body mass, and it is probable that the required ranges of force, power output, etc., for walking are different from those for paddling on the water surface at modest speeds. In that case, musculoskeletal form ought to reflect a compromise between the requirements of walking and swimming. On the whole, it is remarkable that the resonance model comes as close as it does to predicting a value proportional to paddling frequency.

Not all paddling or rowing swimmers appear to operate with a constant frequency mechanism. The stroke frequency of the pleopods of isopod crustaceans (D.E. Alexander, '88) increases with swimming speed. Despite the assertion by Nadel ('77) that competitive human swimmers maintain a constant stroke frequency, reports by Craig et al. ('85) and Toussaint et al. ('83) indicate that human swimmers display a positive relationship between frequency and speed. Even among studies on ducks, there is not agreement. Speed dependence of paddling frequency has been observed by Woakes and Butler ('83) in tufted ducks (Aythya fuligula), and by Baudinette and Gill ('85) in black ducks (Anus superciliosa). In contrast, results of the present study confirm Prange and Schmidt-Nielsen's ('70) report of constant swimming frequency in mallard ducks (Anus platyrhynchos). It was noted that the specimens in the present study would paddle faster than their normal cruising frequencies in order to accelerate within the channel or when straining to escape, and care was taken to analyse only sequences where the animals held constant positions in the channel. Although methodological considerations such as this may account for some variation in measured swimming frequsncies among studies, the possibility remains that different species of ducks use different paddling strategies.

The growth of the lateral gastrocnemius in mallards may be compared with other avian muscles. In a study of growth in young chickens, Helmi

and Cracraft ('77) reported allometric coefficients for three muscles of the thigh that compare favorably with the present study for growth of muscle CSA (range 0.72–0.84), but are generally higher for the longitudinal growth of fibers (range 0.29–0.49). It is unclear whether this difference reflects differing allometries among hind limb muscles or among species, or results from other methodological differences between studies.

The use of "normalized stiffness" to compare the capacities or actions of different muscles has received little attention since its introduction by Houk and Rymer ('81). These authors used this ratio to suggest that the soleus and gastrocnemius muscles of cats had comparable mechanical behavior. Colebatch and McCloskey ('87) normalized their measures of stiffness of human elbow flexors, and found them to agree with equivalent values from the soleus muscles of decerebrate cats, thus supporting a functional role for the tonic stretch reflex in conscious humans. To our knowledge, the present report is the first to use this approach to investigate musculoskeletal function across a range of animal size.

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