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Comparative trends in shortening velocity and force production in skeletal muscles

SCOTT MEDLER
Department of Biology, Colorado State University, Fort Collins, Colorado 80523

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Medler, Scott. Comparative trends in shortening velocity and force production in skeletal muscles. *Am J Physiol Regulatory Integrative Comp Physiol* 283: R368–R378, 2002. First published March 22, 2002; 10.1152/ajpregu.00689.2001.—Skeletal muscles are diverse in their properties, with specific contractile characteristics being matched to particular functions. In this study, published values of contractile properties for >130 diverse skeletal muscles were analyzed to detect common elements that account for variability in shortening velocity and force production. Body mass was found to be a significant predictor of shortening velocity in terrestrial and flying animals, with smaller animals possessing faster muscles. Although previous studies of terrestrial mammals revealed similar trends, the current study indicates that this pattern is more universal than previously appreciated. In contrast, shortening velocity in muscles used for swimming and nonlocomotory functions is not significantly affected by body size. Although force production is more uniform than shortening velocity, a significant correlation with shortening velocity was detected in muscles used for locomotion, with faster muscles tending to produce more force. Overall, the contractile properties of skeletal muscles are conserved among phylogenic groups, but have been significantly influenced by other factors such as body size and mode of locomotion.

skeletal muscle; scaling; shortening velocity; tetanic tension

SKELETAL MUSCLES ARE DIVERSE in their contractile properties, with significant differences existing among and within various animal species. As such, skeletal muscles are striking examples of biological structures adapted for a specific function. Yet skeletal muscles are also highly conserved in terms of the molecular mechanisms responsible for producing muscle contraction (91, 99). Over the last 10 years, a considerable amount of data has been collected on the contractile properties of skeletal muscles from a diverse group of animals. In this study, the contractile properties of >130 skeletal muscles were analyzed to determine what broad trends could be observed that might give insight into the principles of skeletal muscle design. These muscles represent several distinct phylogenic lines, have varied functional demands, and come from animals spanning more than eight orders of magnitude in body mass. Although there have been several excellent reviews summarizing skeletal muscle properties, most focused on terrestrial mammals and none subjected the data to any type of statistical analysis (22, 54, 91, 95). In the present study, maximum shortening velocity (V_{max}) and maximum tetanic tension (P_o) were analyzed with respect to body mass, taxonomic group, mode of locomotion, and compared with one another.

The wide range of shortening velocities is one of the most prominent features that distinguishes muscle fiber types, with values in the present study ranging from ~0.5 muscle lengths (L)/s to nearly 40 L/s. V_{max} is often used to define different fiber types and depends primarily on the type of myosin heavy chain (MHC) expressed by a fiber (91). Fibers with different shortening velocities are found within individual organisms as well as among different species, with the contractile properties being matched to the specific mechanical needs of a particular muscle (86, 87). Integral to these mechanical requirements, muscle power is known to be a function of a muscle's force-velocity profile, with maximum power generally being produced at a V/V_{max} of ~30% (34, 54, 86, 91). Shortening velocity has also been shown to be a major determinant of locomotion energetics, providing an explanation of why small animals use relatively more energy during locomotion than large animals (61, 84). Given the important linkages between shortening velocity and muscle function, it is of interest to examine whether any systematic trends exist among the shortening velocities from different skeletal muscles. Hill (42) predicted that shortening velocity should scale as an allometric function of body mass, with small animals possessing faster, more powerful muscles. This prediction has since been tested, with several studies finding that V_{max} scales with a mass exponent between −0.11 and −0.20 (61, 88, 90, 100). Such scaling effects have been related directly to the different MHCs present in various muscle fibers (82, 91). The activities of glycolytic and oxidative enzymes that fuel locomotory processes also exhibit significant scaling effects in a variety of animals (19, 30, 36). To date, the analysis of shortening velocity has been restricted to terrestrial mammals and it is unclear whether the observed scaling effects are applicable to animals with different phylogenic

Address for reprint requests and other correspondence: S. Medler, Dept. of Biology, Colorado State Univ., Fort Collins, CO 80523 (E-mail: smedler@lamar.colostate.edu).

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histories and modes of locomotion. In the current analysis, I examined whether there were any identifiable trends in V_{max} with respect to body size, taxonomic group, and mode of locomotion.

Unlike V_{max}, P_o is generally considered to be constant among fiber types (91). Nevertheless, there have been inconsistencies in the determination of P_o (91) and several studies documented significant differences related to fiber type (18, 37, 38, 60). P_o is the product of the force produced per cross bridge, the number of cross bridges per unit area, and the muscle's duty ratio (proportion of cross bridges producing force) (91, 94). The type II myosins found in skeletal muscles have a lower duty ratio than other motor proteins as an apparent adaptation for increased speed (44); however, a lower duty ratio also results in lowered force production (44, 85, 94). In this context, the higher duty ratio in smooth muscles is thought to be responsible for the slower, more forceful contractions than those measured in skeletal muscles (7). Rome et al. (85) found that a disproportionate increase in cross bridge detachment rate relative to attachment rate in the toadfish swimbladder muscle (a high-frequency muscle used for sound production) resulted in a significant reduction in the duty ratio and thus force production. This example illustrates that as V_{max} increases, the myosin attachment rate must increase in proportion to the rate of detachment or force production will be impaired (85, 94). It is not currently clear whether any systematic differences in P_o exist among various skeletal muscles.

One of the contributions of comparative physiology has been the detection of underlying principles that unify biology despite the many physiological specializations observed in different animals (92). The goal of this study was to examine broad patterns that transcend the diversity in function often noted in skeletal muscle biology. The scaling of V_{max} with body mass reveals a pattern more general than has been previously appreciated, applying not only to terrestrial mammals but to other terrestrial and flying animals as well. These results suggest that body mass has had a common influence on the shortening velocity of many locomotory muscles, irrespective of phylogenic group. Although maximum force production is more uniform than shortening velocity, a significant correlation was detected between P_o and V_{max}, with faster muscles producing slightly higher forces. In addition, some invertebrate muscles with long sarcomeres (6–15 μm) produce significantly more force than muscles from other animals. Taken together, these findings provide clues to explain some of the principles that influence skeletal muscle design.

MATERIALS AND METHODS

Published values for V_{max} (L/s) and P_o (kN/m^2) were taken from the available literature for 72 species representing several different taxonomic groups, including mammals, birds, reptiles, amphibians, mollusks, insects, and crustaceans (Table 1). When not reported, body masses were estimated from other sources. In some instances, V_{max} was not reported directly, but could be estimated from the reported data. For example, muscle strain and contractile frequencies in some reports were used to estimate shortening velocities. When shortening velocities were not explicitly maximum but were from animals engaged in locomotory activities, I assumed that power was being maximized and that this maximum was reached at 30% of V_{max}. These estimated values are indicated in Table 1.

The relationship between V_{max} and body mass was examined by log transformation of the data and using least-squares linear regression. Several analyses were performed, including an analysis with all of the data, as well as separate analyses with the data segregated by functional group (terrestrial, flying, swimming, and nonlocomotory muscles). When significant relationships were found for the different functional groups, the data for both sets were combined and analyzed using an analysis of covariance (ANCOVA) model to determine whether the regressions were significantly different from one another. When neither the slope nor the elevation were found to differ, the data were pooled and fit with a single regression. Normality was verified by examining frequency histograms of the data and residuals were plotted as a function of mass to ensure that the model was appropriate for the data. In addition, residuals were plotted as a function of experimental temperature to examine whether this additional factor could account for any variability in the data. These residual analyses identified experimental temperature as a significant predictor of V_{max}; therefore temperature was used as second independent variable in multiple regression analyses. The effects of temperature per se were not of primary interest in this study. However, the wide range of experimental temperatures employed in these studies represented a confounding variable that obscured the scaling effects of interest. Including experimental temperature as a second variable in the regression analysis separated temperature effects from the effects of body size, resulting in a more meaningful estimate of the mass exponents.

The relationships between P_o and body mass and between P_o and V_{max} were analyzed by linear regression as described above. Residual analysis of the regression of P_o on V_{max} revealed temperature as a significant predictor of P_o, so temperature effects were partitioned by using a multiple regression analysis. When no significant regressions were detected, P_o values were examined as a function of taxonomic grouping using a Kruskal-Wallis rank test, because the data showed significant departures from normality and equality of variances required for ANOVA. An analog of the Bonferroni pairwise comparison (77) was used to identify groups with significantly different rankings for P_o (experiment-wise $\alpha = 0.05$). Statview 5.0.1 (SAS Institute) was used for all statistical analyses.

RESULTS

A significant ($P < 0.0001$, $r^2 = 0.34$) relationship was found between body mass and V_{max} for all muscles grouped together: $V_{max} = 10.8 \cdot \text{mass}^{-0.17}$ (Fig. 1*A*). Further analyses of these data segregated by functional group (terrestrial, flying, swimming, or nonlocomotory muscles) indicated that the allometry was dominated by the muscles of terrestrial and flying animals (Fig. 1, *B-D*). Muscles from terrestrial animals showed a significant ($P < 0.0001$, $r^2 = 0.61$) relationship with body mass: $V_{max} = 15.9 \cdot \text{mass}^{-0.25}$. A group of data from bird flight muscles measured in vivo was fitted with a separate line, because ANCOVA demonstrated that these V_{max} values were significantly higher than

Table 1.

Common name	Species	Muscle (type)	Mass, g	V_{max}, L/s	P_o, kN/m^2	Temp, °C	Reference
Insects							
Fruit fly	*Drosophila virilis*	dorsal longitudinal (F)	0.0019	38*		22	20
		dorsal ventral (F)	0.0019	37*		22	20
Moth	*Operophtera brucruceata*	flight (F)	0.0300	4	139	18	67
Katydid	*Neoconocephalus triops*	metathoracic (F)	0.100	16.1	136	35	53
		mesothoracic (F)	0.100	12.2	102	35	53
	Neoconocephalus robustus	metathoracic (F)	0.100	11.1	137	35	53
		mesothoracic (F)	0.100	10.1	48	35	53
Dragonfly	*Livellula pulcella*	flight (F)	0.450	9	239	35	32
Bumble bee	*Bombus lucorum*	flight (F)	0.500	18*		40	39
	Bombus terrestris	flight (F)	0.500	16*	36.9	40	55
Locust	*Schistocera americana*	flight (F)	0.500	5.2	363	25	66
Beetle	*Cotinus mutablis*	flight (F)	1.250	13.6		35	56
Hawkmoth	*Manduca sexta*	flight (F)	1.600	10	70	42	67
Roach	*Blaberus discoidalis*	mesothoracic (T)	3.000	5*		25	35
		metathoracic (T)	3.000	7*		25	35
Crustaceans							
Crayfish	*Procambarus clarkii*	abdominal extensor (S)	50	2		21	96
Crab	*Cancer sp.*	claw closer (NL)	50		829.6	25	97
	Menippe mercenaria	claw closer (NL)	50		2200	25	17
	Carcinus maenas	flagellar (NL)	63.5	7.6	8	15	93
	Callinectes sapidus	claw closer (crusher)(NL)	200		638	25	40
		claw closer (cutter) (NL)	200		514	25	40
Lobster	*Nephrops norvegicus*	S_1 (S)	500	0.57		22	43
		S_2 (S)	500	0.45		22	43
	Homarus americanus	fast abdominal (S)	500		83.8	12	45
		slow abdominal (S)	500		451	12	45
		claw closer (NL)	50		390	14	28
		claw closer (NL)	50		425	14	28
Mollusks							
Scallop	*Argopecten irradians*	adductor (S)	29.45	9.89	214	20	78
Squid	*Alloteuthis subulata*	red (S)	500	2.43	262	4	75
Cuttlefish	*Sepia officinalis*	red (S)	500		226	4	75
Fish							
Sculpin	*Myoxocephalis scorpius*	anterior white (S)	100	7.6	159	12	46
		posterior white (S)	100	5.5	161	12	46
		fast (S)	150	5.84		5	47
Carp	*Cyprinus carpio*	red (S)	150	4.65		15	87
		white (S)	150	12.88		15	87
Antarctic cod	*Notothenia coriiceps*	fast (S)	154	1.68		0	33
Blue crevally	*Carangus melampygus*	red (S)	304	4.3	43	30	49
		white (S)	304	7.6	183	30	49
Toadfish	*Opsanus tau*	red (S)	350	2.43	214	16	89
		white (S)	350	4.12	228	16	89
		swim bladder (NL)	350	7.68	56	16	89
Antarctic fish	*Notothenia neglecta*	white (S)	600	3	225	2.5	49
Scup	*Stenotomus chrysops*	red (S)	750	5.55	197	20	23
		pink (S)	750	7.26	151	20	23
Dogfish	*Scyliorhinus canicula*	red (S)	800	0.67		8	2
		white (S)	800	2.34		8	2
		white (S)	450	3.7		12	24
Cod	*Gadus morhua*	red (S)	1,000	0.53		8	2
		white (S)	1,000	1.01		8	2
Grey mullet	*Mugil cephalus*	red (S)	1,137	5.52		30	49
		white (S)	1,137	8.4	210	30	49
Skipjack tuna	*Katsuwonus pelamis*	red (S)	1,200	4.9	24	30	49
		white (S)	1,200	8.1	157	30	49
Kawakawa	*Euthynuus affinis*	red (S)	3,200		25	30	49
		white (S)	3,200		188	30	49
Dolphin fish	*Coryphaena hippurus*	red (S)	11,000	3.1		20	49
		white (S)	11,000	8.2		20	49
Blue marlin	*Makaira nigricans*	red (S)	85,000	2.50	57	25	51
		white (S)	85,000	5.30	176	25	51
Amphibians							
Salamander	*Ambystoma tigrinum n.*	leg extensor (S)	8.62	3.08	339	20	29
Tree frog	*Hyla chrysoscelis*	tensor chodarum(NL)	10	4.7	55	25	73
		sartorius (T)	10	5.2	252.2	25	73

Continued

Table 1—*Continued*

Common name	Species	Muscle (type)	Mass, g	V_{max}, L/s	P_o, kN/m^2	Temp, °C	Reference
	Hyla cinera	tensor chodarum (NL)	10	2.1	180.5	25	73
		sartorius (T)	10	9.8	285.1	25	73
	Hyla versicolor	tensor chodarum (NL)	10	5.2	94.4	25	73
		sartorius (T)	10	7	240.7	25	73
	Osteopilus septenrionalis	sartorius (T)	11.5	10.92	241	30	80
Leopard frog	*Rana pipiens*	semimembranosus (T)	31	12.1	255	25	65
Toad	*Bufo americanus*	white iliofibularis (T)	39	5.8	260	35	50
Clawed frog	*Xenopus laeveus*	5 (S)	100	1.3	302	21.5	57,59
		4 (S)	100	2.6		21.5	59
		3 (S)	100	5.5		21.5	59
		2 (S)	100	8.5	306	21.5	58,59
		1 (S)	100	10.5	367	21.5	58,59
Toad	*Bufo woodhousei*	white iliofibularis (T)	111	5.8	260	30	50
Cane toad	*Bufo marinus*	white iliofibularis (T)	176	6.2	260	30	50
Bullfrog	*Rana catesbeiana*	gluteus magnus (T)	409	4*		20	79
		semimembranosus (T)	409	7*		20	79
Reptiles							
Lizard	*Sceloporus occidentalis*	white iliofibularis (T)	13.7	21.9	187	35	72
Desert iguana	*Dipsosaurus dorsalis*	white iliofibularis (T)	20	20	200	40	69
Terrapin	*Psuedomys scripta*	fast glycolytic (S)	305	5.5	184	15	76
		fast ox/glycolytic (S)	305	3.0	120.4	15	76
		slow (S)	305	1.3	70.6	15	76
Rattlesnake	*Crotalus atrox*	tail-shaker (NL)	420	18.3		35	89
Birds							
Quail	*Coturnix chinensis*	pectoralis (F)	45.7	26*	130.9	40	10
Starling	*Sturnus vulgaris*	pectoralis (F)	71.5	22.3*	122.7	40	16
Japanese quail	*Coturnix coturnix*	latissimus dorsi (F)	125	4.2		25	5
Bobwhite	*Colinus virginianus*	pectoralis (F)	199.5	19.7*		40	98
Chuckar	*Alectoris chukar*	pectoralis (F)	491.5	21*		40	98
Pigeon	*Columba livia*	pectoralis (F)	649	17.1*		40	15
Pheasant	*Phasianus colchicus*	pectoralis (F)	943.4	14.3*		40	98
Mallard	*Anas platyrhynchos*	pectoralis (F)	1,000	12.2*		40	101
		gastrocnemius (T)	1,000	5.9*		40	14
		gastrocnemius (S)	1,000	3.7*		40	14
Chicken	*Gallus domesticus*	white pectoralis (F)	1,500	4.66	165	15	83
		red pectoralis (F)	1,500	2.59	174	15	83
		latissimus dorsi (F)	1,500	0.45	126	15	83
Turkey	*Meleagris gallopavo*	pectoralis (F)	5,275	16*		40	98
Mammals							
Korean bat	*Murina leucogaster*	biceps brachii (F)	7.6	4.8	155	25	21
Mouse	*Mus musculus*	extensor digitorum long. (T)	26	14		37	8
		soleus (T)	26	6		37	8
		diaphragm (NL)	30	15.9		35	63
		internal rectus (NL)	30	20.6		35	63
Guinea pig	*Cavia porcellus*	soleus (T)	130	1.53	147	20	13
Rat	*Rattus norvegicus*	diaphragm (NL)	300	6.20	205	26	48
		1 (T)	380	0.88	73	15	91
		2a (T)	380	2.21	106.5	15	91
		2x (T)	380	2.73	95	15	91
		2b (T)	380	3.11	106	15	91
Cat	*Felis domesticus*	fast (T)	2,500	12.4		35	22
		soleus (T)	2,500	5.2		35	22
Rabbit	*Oryctolagus cuniculus*	inferior oblique (NL)	2,800	19.0	38.6	35	12
		1 (T)	5,000	0.68	106	15	91
		2a (T)	5,000	1.74	116	15	91
		2b (T)	5,000	2.3	132	15	91
Monkey	*Macaca mulatta*	soleus (T)	9,660	0.42	180	15	31
		gastrocnemius (T)	9,660	0.56	180	15	31
		gastrocnemius (T)	9,660	1.41	184	15	31
Dog	*Canis familiaris*	gastrocnemius/plantaris (T)	16,000	3.8		38.5	6
		cricothyroid (NL)	22,500	2.5		37	1
		cricoarytenoid (NL)	22,500	6.7		37	1
Sheep	*Ovis sp*	fast (T)	55,000	0.69		5.5	90
		slow (T)	55,000	0.50		5.5	90
Human	*Homo sapiens*	1 (T)	75,000	0.35	210	15	60
		2a (T)	75,000	1.07	200	15	60
		2b (T)	75,000	3.68	190	15	60

Continued

Table 1—*Continued*

Common name	Species	Muscle (type)	Mass, g	V_{max}, L/s	P_o, kN/m^2	Temp, °C	Reference
Horse	*Equus caballus*	1 (T)	450,000	0.33	84	15	88
		2a (T)	450,000	1.33	97	15	88
		2b (T)	450,000	3.20	120	15	88
Holstein	*Bos sp*	slow (T)	160,000	0.62		5.5	90
		fast (T)	160,000	0.42		5.5	90
Angus-Hereford		fast (T)	500,000	0.63		5.5	90
		slow (T)	500,000	0.30		5.5	90

Muscle types: T, terrestrial; F, flight; S, swimming; NL, nonlocomotory. *Shortening velocities reported were not explicitly maximum, but were from muscles engaged in active locomotion. These values were converted to V_{max} by assuming that these muscles were maximizing power output and that this maximum power was reached at 30% of V_{max}. P_o, maximum tetanic tension; L, muscle length.

the other flight muscles ($P < 0.0001$; Fig. 1*C*). The flight muscles with these data omitted showed a significant ($P < 0.0001$, $r^2 = 0.62$) relationship with body mass: $V_{max} = 8.3 \cdot mass^{-0.20}$ (Fig. 1*C*). The bird flight muscles measured in vivo also showed a significant ($P < 0.024$; $r^2 = 0.60$) scaling relationship with body mass: $V_{max} = 38.6 \cdot mass^{-0.13}$, but with an elevation more than four times that of the other fliers. The slopes of these two lines were not significantly different from one another ($P > 0.63$). ANCOVA revealed that the scaling relationships for muscles used in terrestrial locomotion and in flight (with the indicated bird data omitted) were not significantly different from one another. Therefore, these data were grouped together and analyzed by least-squares regression. These data showed a significant ($P < 0.0001$, $r^2 = 0.65$) relationship with body mass: $V_{max} = 10.2 \cdot mass^{-0.20}$ (Fig. 1*D*). The swimming and nonlocomotory muscles showed no significant scaling effects (Fig. 1, *E* and *F*, respectively). Analyses of the residuals from all of the data and from the terrestrial/flying muscles indicated significant correlations with experimental temperature (Fig. 2, *A* and *B*). Adjusting for the effects of experimental temperature with multiple regression analysis reduced the mass exponent for all of the data from −0.17 to −0.11: $\log V_{max} = 0.306 - 0.11(\log mass) + 0.03(temp$

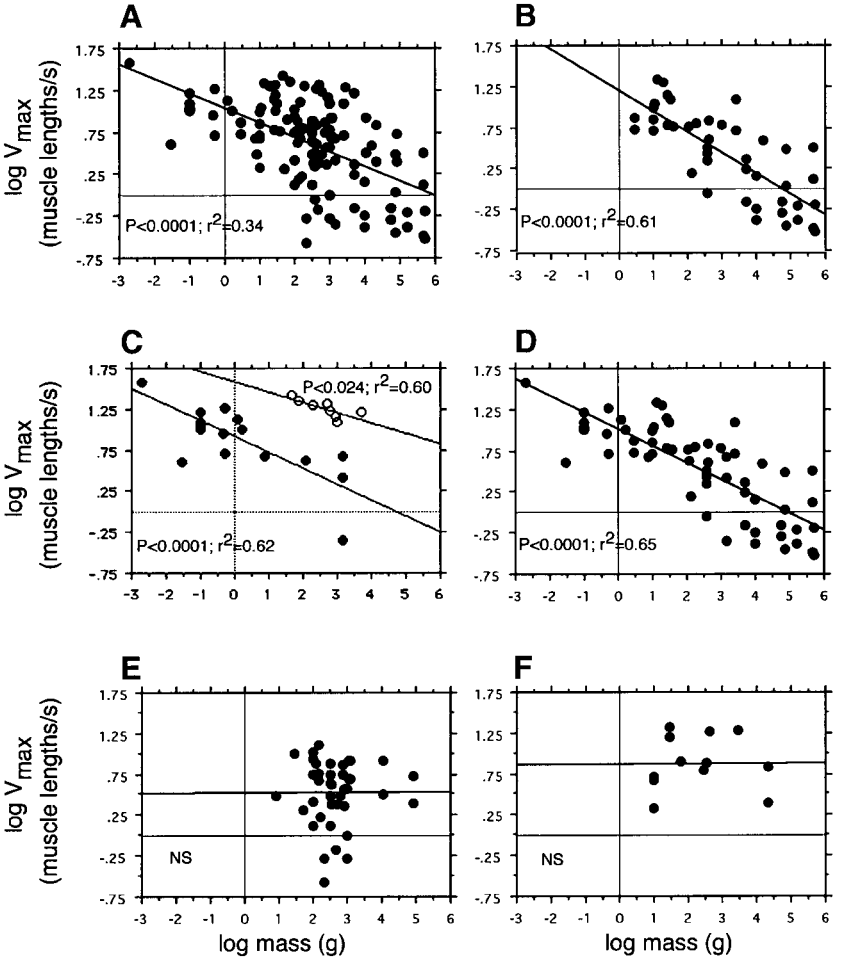

Fig. 1. *A*: maximum shortening velocity (V_{max}) as a function of body mass. All data are grouped together. There was a significant ($P < 0.0001$, $r^2 = 0.34$) relationship between V_{max} and body mass described by the equation: $V_{max} = 10.8 \cdot (mass)^{-0.17}$. *B*: data for muscles used in terrestrial locomotion. There was a significant ($P < 0.0001$, $r^2 = 0.61$) relationship between V_{max} and body mass: $V_{max} = 15.9 \cdot (mass)^{-0.25}$. *C*: data for muscles used in flight, with the data collected from birds in vivo fit with a separate regression equation (○). There was a significant ($P < 0.024$; $r^2 = 0.60$) scaling relationship between V_{max} and body mass for the bird flight muscles measured in vivo: $V_{max} = 38.6 \cdot (mass)^{-0.13}$. The relationship for the rest of the fliers (●) was also significant ($P < 0.0001$, $r^2 = 0.62$) but had an elevation more than four times less than for the birds: $V_{max} = 8.3 \cdot (mass)^{-0.20}$. The slopes of these two lines were not significantly different from one another ($P > 0.63$). *D*: data for muscles used in flight and terrestrial locomotion pooled. Analysis of covariance indicated that the regression lines from these 2 groups were not significantly different from one another. There was a significant ($P < 0.0001$, $r^2 = 0.65$) relationship between V_{max} and body mass for these data: $V_{max} = 10.2 \cdot (mass)^{-0.20}$. There was no significant relationship between V_{max} and body mass in muscles used for swimming (*E*) nor for nonlocomotory muscles (*F*).

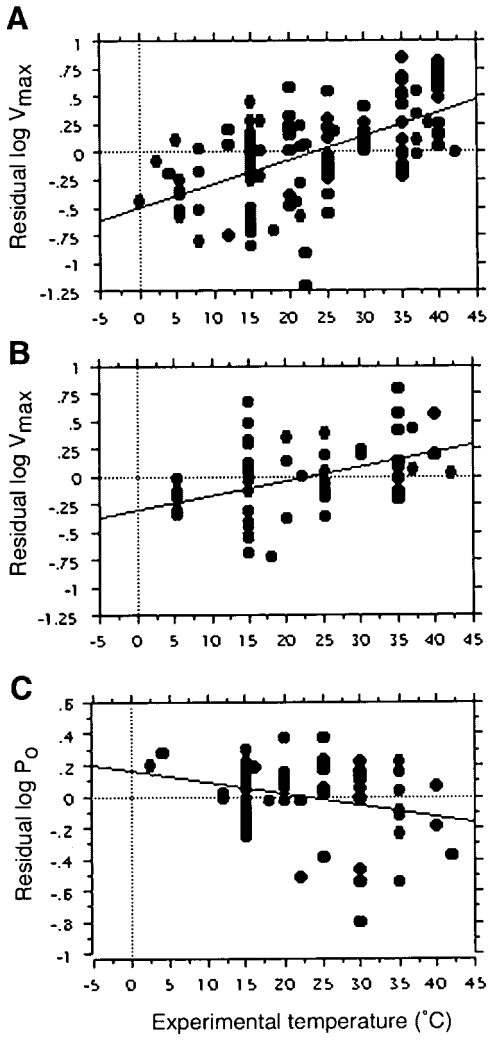

Fig. 2. Residuals from the regression analyses as a function of experimental temperature. *A*: residuals from all data (Fig. 1*A*) showed a significant ($P < 0.0001$; $r^2 = 0.32$) positive correlation with experimental temperature. Adjusting for the effects of different experimental temperatures using multiple regression reduced the mass exponent from −0.17 to −0.11: log V_{max} = 0.306 − 0.11(log mass) + 0.03(temp °C) ($P < 0.0001$; $r^2 = 0.57$). *B*: residuals from the terrestrial/flying data (Fig. 1*D*) showed a significant ($P < 0.0001$; $r^2 = 0.22$) positive correlation with experimental temperature. Adjusting for the effects of different experimental temperatures reduced the mass exponent from −0.20 to −0.12: log V_{max} = 0.19 − 0.12(log mass) + 0.03(temp °C) ($P < 0.0001$; $r^2 = 0.78$). *C*: residuals from the regression of maximum tetanic tension (P_o) as a function of V_{max} (Fig. 3*A*) showed a significant ($P < 0.025$; $r^2 = 0.08$) negative correlation with experimental temperature. Adjusting for experimental temperature differences increased the V_{max} exponent from 0.14 to 0.28: log P_o = 2.28 + 0.28(log V_{max}) − 0.01(temp °C) ($P < 0.003$; $r^2 = 0.18$).

°C) ($P < 0.0001$; $r^2 = 0.57$). Similarly, after the effects of different temperatures in the terrestrial/flying data were accounted for, the mass exponent was reduced from −0.20 to −0.12: log V_{max} = 0.19 − 0.12(log mass) + 0.03(temp °C) ($P < 0.0001$; $r^2 = 0.78$).

There was no relationship between P_o and V_{max} for all of the data together (not shown). However, there was significant ($P < 0.039$; $r^2 = 0.07$) correlation between P_o and V_{max} for locomotory muscles, with faster muscles tending to produce higher forces: $P_o = 122\ V_{max}^{0.14}$ (Fig. 3*A*). A residual analysis indicated that experimental temperature was also a significant predictor of P_o ($P < 0.03$; $r^2 = 0.07$; Fig. 2*C*); therefore temperature was entered into the regression to account for the influence of experimental temperature. Including temperature in the model resulted in an increase in the V_{max} exponent from 0.14 to 0.28: log P_o = 2.28 + 0.28(log V_{max}) − 0.01(temp °C) ($P < 0.003$; $r^2 = 0.18$). There was no significant relationship between body mass and P_o (Fig. 3*B*). However, P_o was found to be significantly higher in the crustaceans, amphibians,

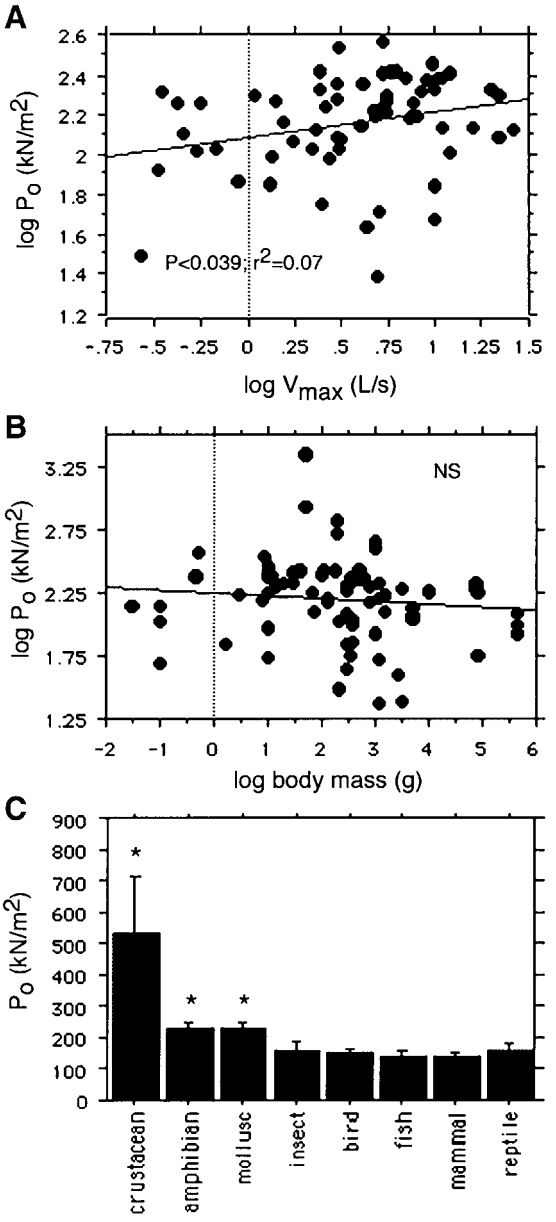

Fig. 3. P_o as a function of V_{max}, mass, and taxonomic group. *A*: P_o from locomotory muscles showed a significant ($P < 0.032$; $r^2 = 0.07$) increase as a function of V_{max}: $P_o = 122 \cdot V_{max}^{0.14}$. *B*: P_o showed no relationship with body mass. *C*: P_o was significantly ($P < 0.05$) higher (*) in muscles from crustaceans, amphibians, and mollusks than in muscles from other taxonomic groups as indicated by a Kruskal-Wallis rank test (mean ± SE).

and mollusks than in the other taxonomic groups (Fig. 3*C*).

DISCUSSION

It has long been recognized that smaller animals tend to have faster muscles than larger animals (42, 74). Hill (42) proposed that animals of differing size possess relative differences in limb dimension as a result of geometric scaling, predicting that shortening velocity should scale to match the natural frequency of the limbs, which in turn should scale as mass$^{-0.33}$. Others have argued that animals do not scale geometrically, but that limb dimensions scale according to the principles of elastic similarity and that V_{max} scales as mass$^{-0.125}$ (74). The results presented here support the hypothesis that V_{max} in terrestrial and flying animals scales very close to mass$^{-0.125}$. When experimental temperature is included in the regression model, V_{max} in the terrestrial and flying animals scales as mass$^{-0.12}$. Likewise, shortening velocity scales as mass$^{-0.13}$ in the bird flight muscles measured in vivo. These results are also consistent with other studies that have found V_{max} to scale as mass$^{-0.13}$ (90) or as mass$^{-0.11}$ (100) in skeletal muscles measured under uniform experimental conditions. An assumption common to current explanations of this allometry is that the natural frequency of limb movement is derived from the physical constraints of scale and that shortening velocity has been selected to match the natural frequency of the limbs (42, 61, 74, 88, 90, 100). Fairly consistent with this assumption, stride frequency has been shown to scale as mass$^{-0.15}$ in running mammals (41), wing beat frequency in birds scales as mass$^{-0.33}$ (81), and cycle frequency for a number of invertebrates scales approximately as mass$^{-0.20}$ (34). Nevertheless, the assumption that V_{max} has evolved to match contractile frequency is probably overly simplistic, inasmuch as shortening velocity is only one determinant of contractile frequency (8, 69, 70). Shortening deactivation and inertial load, for example, are other factors that affect contractile frequency (70). Therefore, V_{max} is likely an important, but not exclusive, factor that sets frequency.

Whatever the precise mechanisms involved, the current study demonstrates that the scaling relationship is more universal than previously appreciated, applying not only to terrestrial mammals, but to a wide variety of animals and locomotory mechanisms. In fact, 65% of the variability in V_{max} can be accounted for by body mass alone in the group comprised of terrestrial and flying animals ($r^2 = 0.65$) and this value increases to 78% when experimental temperature is factored into the model. Such a strong correlation might be viewed as surprising, given the wide array of functional demands of different skeletal muscles that are used not only as motors but also as struts, brakes, and springs (25, 34, 71). Much of the variability remaining in the data is probably a consequence of these different functional requirements. For example, Rome and colleagues (87) demonstrated that carp possess fast and slow fiber types that differ in shortening velocity by a factor of about three. These different muscle types are coupled to specific biomechanical orientations that either drive slow swimming or fast starts. As such, the fast and slow muscles function as different gears to power specific types of locomotion (87). Likewise, mammalian fibers exhibit several-fold differences in shortening velocity between the fastest and slowest fibers within a given species (Table 1).

Interestingly, even muscles not directly responsible for locomotion can be influenced by locomotory processes. A case in point, the natural frequency of diaphragm muscles in terrestrial mammals is matched with that of stride frequency, reflecting the need to coordinate respiration with movement (4, 103). It would not be surprising to find that shortening velocity in these muscles scales to match locomotory processes, even though the diaphragm is not used for locomotion. Such correlation will tend to reinforce the observed scaling effects, even when the muscles are not directly powering locomotion, but may be acting in other roles such as joint stabilization. The allometries observed for flying and terrestrial animals (Figs. 1, *B-D*) are particularly interesting when compared with the lack of any scaling in the swimming and nonlocomotory muscles (Fig. 1, *E* and *F*, respectively). This juxtaposition suggests that common elements in the physical constraints of weight-bearing animals have had convergent or conserved effects on their locomotory systems.

The muscles used for swimming are conspicuously different from other muscles used for locomotion, with shortening velocities that do not appear to be influenced by body mass. Previous data on the scaling of shortening velocity in swimming muscles have been sparse and equivocal. James et al. (46) found V_{max} for fast muscles in *Myoxocephalus scorpius* scales with a mass exponent of about −0.10 and tail beat frequencies in cod were found to scale with a similar mass exponent of about −0.16 (estimated from Ref. 3 assuming fish length = mass$^{0.31}$). In addition, myofibrillar ATPase activity has been shown to decrease as a function of size in several teleost species (102). In contrast, Curtin and Woledge (24) found the shortening velocity of dogfish muscles to be scale independent. It is tempting to speculate that the apparent scale independence of shortening velocity is related to the effects of neutral buoyancy, but there may also be artifacts of the data that obscure significant trends. For example, the largest swimmers in the data set are fast-swimming pelagic fish that could be expected to possess faster muscles than the other animals. In addition, the body mass range for this group is much narrower than for the flying and terrestrial animals, making significant scale effects more difficult to detect. Nevertheless, the flying and terrestrial muscles still show a significant scaling effect over the more limited mass range of the swimming muscles ($P < 0.0001$; data not shown). Further work is needed to clarify the pattern for swimming muscles revealed in the current study.

The in vivo data from bird flight muscles also present an intriguing exception to the allometry of other flying

and terrestrial muscles. These data were collected using strain gauges implanted in the flight muscles (10, 11, 15, 16, 98, 101) and although the shortening velocities show a scaling effect similar to the other locomotory muscles (mass exponent of −0.13), the regression line is significantly higher than that of the other flying and terrestrial muscles. It is interesting that during flight, the pectoral muscles experience a rapid stretch immediately preceding the contraction producing the downstroke of the wings. This prestretch to 110–125% of resting muscle length is often even greater in magnitude than the change in length experienced during shortening (15, 98, 101). Prestretch of muscle fibers is known to enhance force production (8, 26, 27) and such enhancement has been implicated as an important mechanism for increasing power output during locomotion (8, 101). It may be that this stretch is related to the enhanced shortening velocity as well. A related possibility is that the assumption of power being maximized at V/V_{max} of 30% is not be valid for these muscles. Storage of elastic energy in the muscles and tendons may act to amplify power output and these muscles may be operating at a V/V_{max} of much greater than 30%. Peplowski and Marsh (80) demonstrated that the power output from tree frogs during jumping was at least seven times higher than predicted from the contractile properties of isolated leg muscles. Their interpretation was that elastic components of the musculoskeletal system were being used to amplify power output. Whatever the reason for the discrepancy between the in vivo bird data and the rest of the values, there is clearly a need for both in vitro and in vivo data to obtain a full understanding of avian flight muscles (86). This need stems from the principle that muscles operate differently in vivo than under experimentally imposed conditions (8, 9, 70, 71). In a recent set of studies, the first comparisons of in vitro and in vivo function of bird flight muscles have become available (10, 11). The authors cite preliminary results from in vitro measurements suggesting a V/V_{max} of 0.24 and a V_{max} of 32 L/s for these flight muscles (10). These values are in good agreement with the estimates used in the current study, but more studies of this type are needed to reveal how the flight muscles of birds may differ from other skeletal muscles.

Many animals change body mass by several orders of magnitude during ontogeny, and the current study suggests that V_{max} should decrease as an animal increases in size. Consistent with this prediction, James et al. (46) found that shortening velocity decreased as a function of mass in the swimming muscles of the shorthorn sculpin, with shortening velocity scaling as $mass^{-0.10}$. A detailed protein analysis revealed a shift in the troponin I isoforms in larger animals, with no detectable changes in MHC isoforms. Likewise, myofibrillar ATPase activity in other teleost fish slows as fish increase in size (102), but no information is available about the molecular changes responsible for this slowing. Marsh (69) similarly found that larger lizards possess slower muscles, with V_{max} scaling as $mass^{-0.084}$, but again, no analyses were performed to examine the molecular changes responsible for the adjustments in contractile properties. It is currently unknown how general such changes during growth may be and the mechanisms responsible for these changes remain obscure. Nevertheless, changes in V_{max} likely require the switching of myofibrillar isoforms during growth and development. A recent study of ontogenic changes in dragonfly flight muscles provides an excellent example of the type of study that might be applied to the questions presented here (68). In these flight muscles, alternative splicing of Tn-T transcripts was found to produce significant changes in wing beat frequency and power output resulting from changes in Ca^{2+} sensitivity (68). Such fine tuning of myofibrillar proteins during growth in animals exhibiting extremes in mass should provide interesting models of muscular plasticity in the future.

Finally, the current analyses demonstrate that muscle force production is more constant than shortening velocity, but that significant differences do exist, with faster muscles producing slightly greater forces (Fig. 3*A*). Although this trend was statistically significant ($P < 0.039$), the correlation between force production and contractile velocity was weak ($r^2 = 0.07$) and was likely due to differences in relative myofibrillar volumes. It is expected, for example, that fast glycolytic fibers will possess a relatively higher myofibrillar volume and thus produce greater forces than slow oxidative fibers (62). The slightly higher P_o values for the amphibians and mollusks may also be related to such differences. In contrast, the higher force production in some crustacean muscles arises because their long-sarcomered fibers (6–15 μm) possess a higher number of myosin cross bridges per sarcomere (52, 97). The reduced force production related to a lowered duty ratio in some high-frequency muscles (85) does not appear to be a general phenomenon linked to shortening velocity. Overall, the relative constancy of force per cross-sectional area underscores the conserved nature of the myosin molecule. It seems likely that the amount of force produced per myosin cross bridge is a highly conserved trait that became optimized early in the evolution of the myosin molecule.

Although skeletal muscle is often touted for its diversity and specialization, in the broadest sense, skeletal muscles are conserved in their contractile properties. Recent molecular analyses demonstrate that sequence divergence is restricted to limited regions of the MHC molecule and that a greater degree of similarity exists among orthologous MHCs (i.e., human MHC I/mouse MHC I) than among paralogous MHCs (i.e., MHCs I, IIa, IIb, IIx within a species) (64, 99). These patterns indicate that functional demands are generally more important than phylogenic history in determining myosin structure and function. The results of the current analysis are consistent with this interpretation, as body mass and functional requirements (terrestrial, flying, swimming, or nonlocomotory) are significant predictors of shortening velocity that transcend differences related to phylogeny. These factors have produced convergent or conserved pat-

terns in the contractile properties of skeletal muscles in a diverse group of animals. The principle pattern revealed here is that the influence of body size on the shortening velocity of skeletal muscles is more general than previously recognized. It is not only the muscles of mammals, but muscles from a wide variety of flying and terrestrial animals that conform to this same allometry. This scaling effect is in sharp contrast to the scale independence of shortening velocity in swimming and nonlocomotory muscles. This juxtaposition suggests that weight-bearing animals in particular have been significantly influenced by common constraints during the evolution of a variety of specific locomotory mechanisms. Integrative and comparative approaches have identified several general principles of locomotion and muscle design common to diverse animals (25, 86) and such approaches will continue to play an important role in our understanding of skeletal muscle function.

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