

FLIGHT MUSCLE CONTRACTION IN RELATION TO AMBIENT TEMPERATURE IN SOME SPECIES OF DESERT BATS

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Abstract—The properties of motor activity over a wide range of temperatures for 5 species of bats compared to a homeotherm and poikilotherm revealed the following:

1. Force contraction of poikilotherms increase with a decrease in temperature. For homeotherms, force contraction remains relatively constant, losing contractability between 12° and 5°C. For bats, force contraction remains relatively constant over the entire test range of temperatures.
2. Twitch duration increased for all species of animals tested, but for bats, the magnitude of duration was greater as temperatures were reduced.
3. There was an inverse relationship between muscle size and force contraction for the bat species tested.
4. The adaptive significance of motor activity at various temperatures is discussed with regard to known ecological behavior.

INTRODUCTION

Muscle performance over a range of ambient temperatures has received little attention (Walker, 1950; Hill, 1970 and Prosser, 1973). Past studies have dealt only with laboratory and domestic animals. Studies over the last few years have shown that some bats, particularly those in the SW United States, are capable of periodic activity during the winter (O'Farrell *et al.*, 1967 and O'Farrell & Bradley, 1970) and maintenance of flight at significantly reduced body temperatures (Bradley & O'Farrell, 1969; Studier & O'Farrell, 1972 and Hirshfeld & O'Farrell, 1976). From these studies, it is apparent that flight muscles of these bats are capable of coordinated and sustained activity over a wide range of temperatures (22–36°C).

The present study is an examination of muscle contractability in low temperature fliers over a wide range of ambient temperatures. We have further attempted to compare these findings with similar data obtained on a homeotherm and poikilotherm.

MATERIALS AND METHODS

The animals used in this study were: The Western Pipistrelle, *Pipistrellus hesperus*; the California Myotis, *Myotis californicus*; the Pallid Bat, *Antrozous pallidus*; Townsend's Big-eared Bat, *Plecotus townsendii*; the Brazilian Free-tailed Bat, *Tadarida brasiliensis*; the Bullfrog, *Rana catesbeiana*; and Wistar Laboratory Rat, *Rattus* sp. Vernacular names of bats follow the system of Jones *et al.* (1973).

Bats used in this study were collected from various locations in S Nevada and N Arizona (600–2500 m elevation) from July and August 1975, and were tested within 2 days of collection. Forearm extensors were excised, measured to the nearest 0.1 mm, and weighed to the nearest 0.1 mg. The muscle was then attached to a type B skeletal muscle myograph and suspended in a muscle warmer filled with either mammalian or amphibian physiological saline. The muscle warmer was placed in a temperature controlled water bath at an ambient temperature (T_a) of 36°C, and monitored by a thermistor within the muscle warmer and

attached to a YSI tele-thermometer. The myograph was attached to a Narco Biosystems Rectilinear table top physiograph.

To minimize error due to different muscle sizes, the tension was set before each test to approximately the same pen position on the physiograph. Some error could occur since optimum length for contraction was not determined for each muscle, but all muscles were set at the same proportionate length. Standard physiograph settings for all experiments were: filter 3K; frequency 5; duration 10 m sec; and chart speed 0.5 cm/sec. Resistance (Ω mV/cm) was determined for each test, as were maximal and sub-maximal stimuli. Unless otherwise stated, muscles received maximal stimulation.

Except where noted, each experiment began at 36°C, then was lowered to 4°C, and raised back to 36°C. At 4°C intervals along this gradient, the muscle was stimulated and the twitches recorded, usually 3 twitches/ T_a interval. An additional test run was conducted by bubbling oxygen through the physiological saline and, in one instance, reversing the muscle temperature gradient.

Measurements taken from muscle twitch recordings were mean peak heights to the nearest 0.1 mm and duration. Duration was determined by using the greatest change in slope, during relaxation, as the end point. Force exerted in gram weight (g wt) was determined for each resistance used by suspension of varying weights from the myograph (Hill, 1970). Force contraction (FC) in g wt/cm² was calculated using the formula:

$$FC = (P/l_o)/M$$

where P is force exerted in g wt, l_o is muscle length in cm, and M is muscle mass in g (Hill, 1970; Carlson & Wilkie, 1974). The values given in Table 1 were used in calculations for the respective species. Mean weights and lengths of muscles for each species were used, since high and low ranges fell within the confidence intervals of 2 S.E. Statistical significance was set at the 0.05 level.

RESULTS

Rana catesbeiana had maximum FC from 16° to 8°C, approaching 100 g wt/cm² (Fig. 1). *Rattus*

Table 1. Mean weights (mg) and lengths (mm) of various forearm extensor muscles. N = number of individual muscles. 2 S.E. _{\bar{x}} are given in parentheses

Species	N	Weight	Length	Muscle
<i>Pipistrellus hesperus</i>	9	3.0 (0.6)	14.8 (1.0)	Extensor carpi radialis longus
<i>Myotis californicus</i>	8	6.7 (0.8)	18.1 (1.2)	Extensor carpi radialis longus
<i>Tadarida brasiliensis</i>	14	19.4 (2.2)	23.3 (1.0)	Extensor carpi radialis longus
<i>Plecotus townsendii</i>	6	21.9 (4.2)	22.2 (4.8)	Extensor carpi radialis longus
<i>Antrozous pallidus</i>	12	38.7 (3.8)	28.8 (1.6)	Extensor carpi radialis longus
<i>Rana catesbeiana</i>	2	170.8	13.0	Extensor digitorum communis
<i>Rattus</i> sp. (sub-adult)	2	305.7	18.0	Extensor carpi radialis
(juvenile)	2	19.7	8.0	Extensor carpi radialis

reached maximum *FC* at 36°C, approaching 70 g wt/cm², followed by a gradual decrease and loss of contractability at 8°C (Fig. 1). The sub-maximal trial of *Rattus* was more variable with maximum *FC* at 32°C and 300 g wt/cm², losing contractability at 3°C. Maximal and sub-maximal trials of *Rattus* are not comparable since animals of different age and size were used. *Tadarida brasiliensis*, a high temperature flier (Studier & O'Farrell, 1972) had maximum *FC* at 28°C, approaching 1300 g wt/cm² (Fig. 1).

Bat species capable of low temperature flight tended to show higher *FC* than homeotherms or poikilotherms (Fig. 2). *Antrozous pallidus* exhibited stable *FC* with the maximum *FC* approaching 850 g wt/cm² at 36, 32, and 4°C (Fig. 2). *Plecotus townsendii* exhibited maximum *FC* approaching 1250 g wt/cm² at 36°C (Fig. 2). The only significant difference of *FC* between *A. pallidus*, *T. brasiliensis* and *P. townsendii* was at 24 and 16°C. *Myotis californicus* exhibited stable *FC* with maximum values approaching 2200 g wt/cm² at 32°C (Fig. 2). *Pipistrellus hesperus* exhibited the greatest *FC*, approaching 5100 g wt/cm² at 32°C on the sub-maximal stimulation (Fig. 2). The greatest

amount of variability was observed in this species. Maximal trial results were reduced, but were only significantly different at temps <28°C. For the low temp fliers, *FC* was uniform over the entire temp range tested.

Data for Figs 1 & 2 present only the initial downward portion of the trials, since the upward portion exhibited similar trends up to 30°C, at which time muscle contractability deteriorated. Temperature stress and O₂ depletion were then examined as 2 factors which could possibly affect loss of muscle contractability. When O₂ was added to the saline, *FC* was somewhat elevated. The muscle also was stimulated to 42°C before loss of contractability, maintaining a stable *FC* until 36°C (Fig. 3). Although O₂ depletion seemed to be an important factor in *FC*, temperature stress appeared to be an even greater factor as evidenced by the increased *FC* values beginning at low temperatures (Fig. 3).

Muscle twitch duration was similar in all species studied except for *Rattus*, which lost all muscle contractability below 12°C with no signs of recovery (Fig. 4). Maximum duration achieved by *Rattus* was

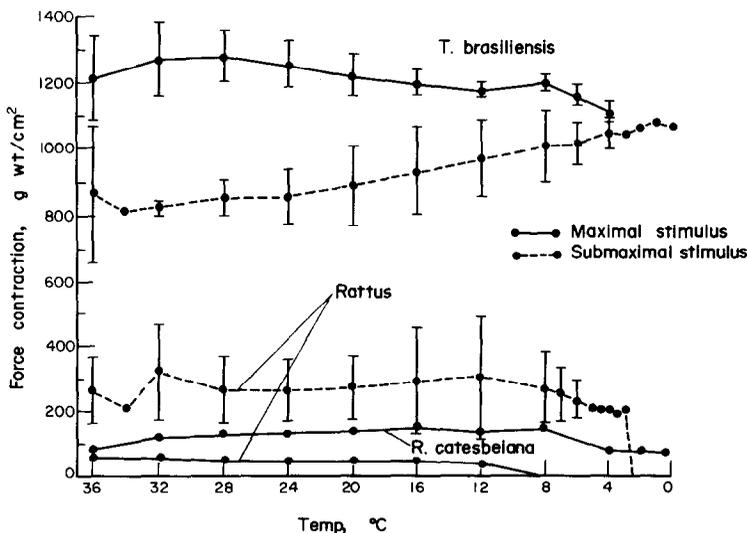


Fig. 1. Mean force contraction (g wt/cm²) of forearm extensors over a range of muscle temperatures for *Tadarida brasiliensis*, *Rattus* (Wistar Strain), and *Rana catesbeiana*. Vertical bars represent ± 2 S.E. _{\bar{x}} .

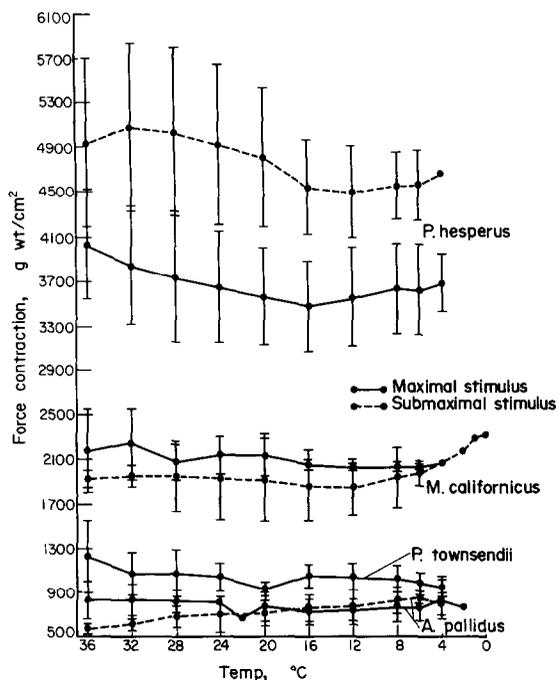


Fig. 2. Mean force contraction (g wt/cm²) of forearm extensors over a range of muscle temperatures for *Pipistrellus hesperus*, *Myotis californicus*, *Plecotus townsendii*, and *Antrozous pallidus*. Vertical bars represent ± 2 S.E. \bar{x} .

approx 0.25 secs at 12°C, whereas *R. catesbeiana* had maximum duration of 3.2 secs at 2°C. Muscle twitch duration for all species of bats were similar until approx 16°C, at which time duration of *M. californicus*, *P. hesperus*, and *T. brasiliensis* increased greatly (Fig. 4). Durations of *A. pallidus* and *P. townsendii* showed a response that was closer to *R. catesbeiana* than all other species of bats. In *R. catesbeiana*, between 0 and 8°C on the upward portion, no twitch was elicited (Fig. 4).

An actual trial illustrates the differences of muscle contractability for *Rattus*, *A. pallidus*, and *R. cates-*

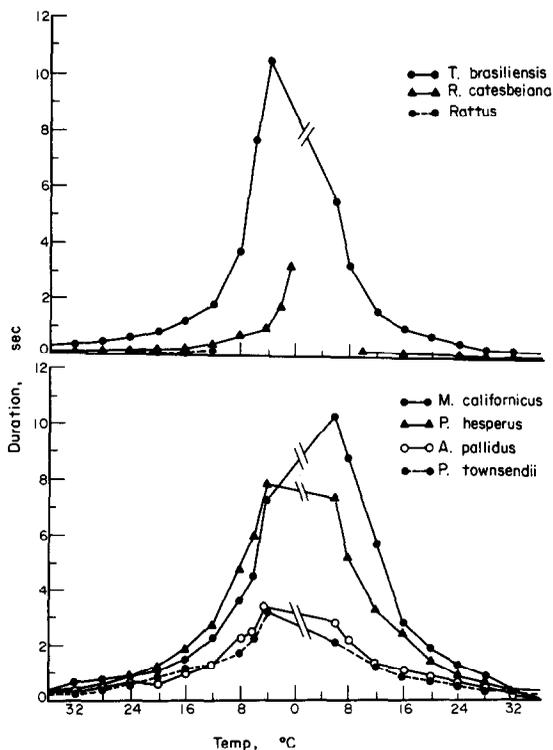


Fig. 4. Mean twitch duration (sec) of forearm extensors over a range of muscle temperatures for *Tadarida brasiliensis*, *Rana catesbeiana*, *Rattus* (Wistar Strain), *Myotis californicus*, *Pipistrellus hesperus*, *Antrozous pallidus* and *Plecotus townsendii*. Broken lines indicate temperatures during which muscles were not stimulated. Open areas indicate temperatures during stimulation at which no twitch was elicited.

beiana over a range of temperatures (Fig. 5). Peak heights, representative of FC, for *A. pallidus* is closer to *R. catesbeiana* than *Rattus*, whereas muscle twitch duration was unlike either species.

There appears to be an inverse relationship between FC and muscle wt (see Table 1; Figs 1 & 2). Such a trend has been noted in a number of other animals (Henneman & Olson, 1965).

DISCUSSION

There is little available comparative information for maximum force contraction over a wide temperature range. Hill (1970) gives comparative values in g wt/cm², but other workers (Walker, 1949) used non-comparative values for force contraction which cannot be converted to g wt/cm². Our data correspond to that of Hill (1970; see Table 2, this study); however, he used a sartorius which possesses inherently different characteristics than an extensor digitorum communis (Prosser, 1973). Comparative values for homeotherms (Table 2) indicate high force contraction at approximate body temperatures, except for the present study. Although our experimental animals were not comparable, the trend is apparent that with decreasing temperatures, there is a reduction in force contraction. The bats used in the present study showed high force contraction at all temperatures tested (Table 2; Figs 1 & 2). The trends are similar

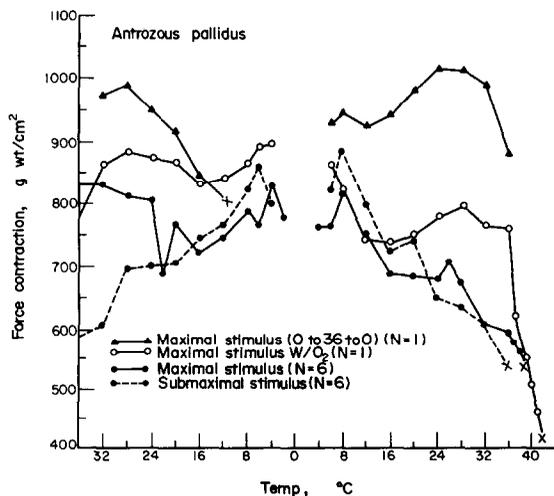


Fig. 3. Mean force contraction (g wt/cm²) of forearm extensors over a range of muscle temperatures for *Antrozous pallidus*. X = end of muscle response.

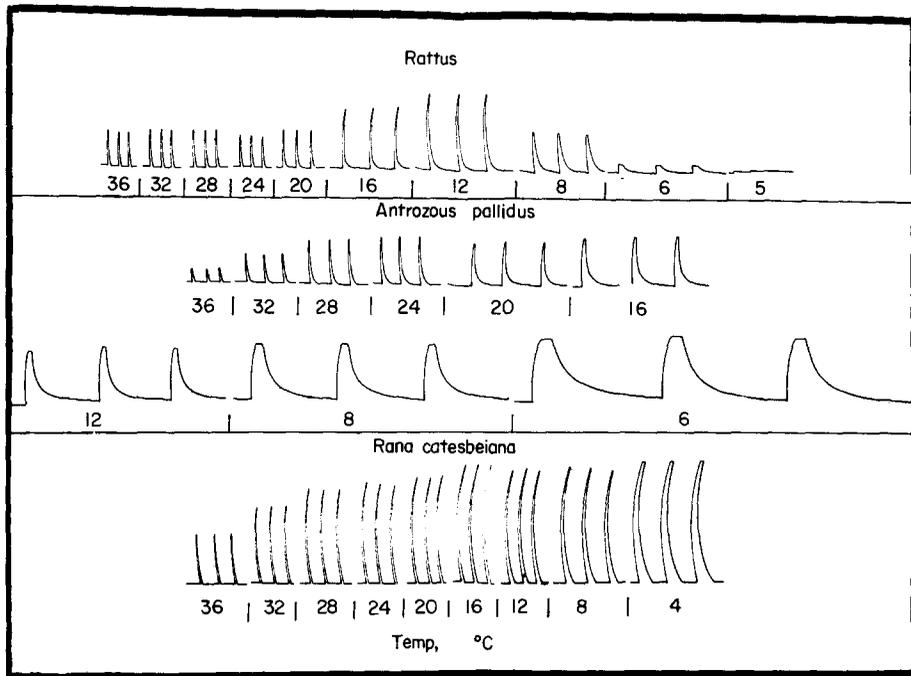


Fig. 5. Sample test run showing changes in response of *Rattus* (Wistar Strain), *Antrozous pallidus*, and *Rana catesbeiana* forearm extensors during stimulation as muscle temperature is reduced.

for all mammals tested to 12°C; below 8°C the pattern exhibited by bats were most similar to that exhibited by *Rana* (Figs 1 & 2). Henneman & Olson (1965) noted the variability between types of muscle and contractile characteristics. We believe this accounts for much of the differences observed between our study and previous studies. Our purpose in using forearm extensors was to test an important locomotor muscle for bats that is normally subjected to a wide range of temperatures. Therefore, the com-

parisons within the present study should be valid with regard to fundamental contractability.

There is a discrepancy between force contraction with maximal and submaximal stimulation for *P. hesperus* and *Rattus* (Figs 1 & 2). The *Rattus* used during maximal stimulation was a 150 g subadult, whereas the submaximal test run was conducted on a 25 g juvenile. Prosser (1973) noted that younger animals exhibited longer twitch duration than older animals which may account for the differences in the present

Table 2. Maximum force contraction (FC; g wt/cm²) developed by muscles at selected temperatures (T; °C). EDL = extensor digitorum longus; ECR = extensor carpi radialis; SR = sartorius; EDC = extensor digitorum communis; ECRL = extensor carpi radialis longus. Animals chosen from this study for comparison indicate a representative cross-section

Species	Muscle	T	FC	Cite
<i>Felis domesticus</i> (newborn)	EDL	34.7	1270	Close & Hoh, 1967
<i>Rattus</i> sp. Wistar Strain	EDL	35.0	2870	Close, 1969
<i>Rattus</i> sp. Wistar Strain	ECR	36.0	54	This study
<i>Rattus</i> sp. Wistar Strain	ECR	12.0	36	This study
Frog*	SR	0.0	175	Hill, 1970
<i>Rana catesbeiana</i>	EDC	36.0	88	This study
<i>Rana catesbeiana</i>	EDC	8.0	158	This study
<i>Tadarida brasiliensis</i>	ECRL	36.0	1210	This study
<i>Tadarida brasiliensis</i>	ECRL	8.0	1202	This study
<i>Antrozous pallidus</i>	ECRL	36.0	830	This study
<i>Antrozous pallidus</i>	ECRL	8.0	775	This study
<i>Pipistrellus hesperus</i>	ECRL	36.0	4030	This study
<i>Pipistrellus hesperus</i>	ECRL	8.0	3630	This study

* Species not reported.

Table 3. Duration of twitch (D:sec) developed by muscles at selected temperatures (T:°C). EDL = extensor digitorum longus; FDL = flexor digitorum longus; ECR = extensor carpi radialis; TS = triceps surae; GA = gastrocnemius; SR = sartorius; EDC = extensor digitorum communis; ECRL = extensor carpi radialis longus. Animals chosen from this study for comparison indicate a representative cross-section

Species	Muscle	T	D	Cite
<i>Felis domesticus</i> (newborn)	EDL	34.7	0.10‡	Close & Hoh, 1967
<i>Cavia procellus</i> Hartley Strain	FDL	36-38	0.04‡	Barnard <i>et al.</i> , 1971
<i>Rattus</i> sp. Wistar Strain	EDL	34.5-35.5	0.02‡	Close, 1969
<i>Rattus</i> sp. Wistar Strain	ECR	36	0.12	This study
<i>Rattus</i> sp. Wistar Strain	ECR	12	0.23	This study
<i>Rattus</i> sp. (newborn) Wistar Strain	EDL	35-36	0.11‡	Close, 1964
<i>Rattus</i> sp. Anheuser Busch Strain	TS	22†	0.17‡	Walker, 1949
Frog*	GA	12	0.15‡	Walker, 1949
<i>Rana catesbeiana</i>	EDC	36	0.11	This study
<i>Rana catesbeiana</i>	EDC	8	0.69	This study
<i>Tadarida brasiliensis</i>	ECRL	36	0.33	This study
<i>Tadarida brasiliensis</i>	ECRL	8	3.62	This study
<i>Antrozous pallidus</i>	ECRL	36	0.21	This study
<i>Antrozous pallidus</i>	ECRL	8	2.17	This study

* Species not reported.

† Rectal temperature.

‡ Duration recorded at 1/2 relaxation.

study (Fig. 1). *P. hesperus* females were examined during July and August. No males were captured during the course of this study. Field experiments showed that during August, the animals were in poor physiological condition and unable to sustain flight when artificially stressed. We believe the variability in physical condition at the time of testing may explain the discrepancy between submaximal and maximal response in this species (Fig. 2).

Duration of twitches for all animals tested at higher temperatures was short with increased duration as temperatures were reduced (Table 3). Again, comparisons are difficult due to the differences in muscles used. Where comparisons at different temperatures are possible, it is evident that lower temperatures have a greater effect on forearm extensors than the gastrocnemius. Twitch duration over the entire range of experimental temperatures (Fig. 4) showed a poikilothermic response in bats. It should be noted that *Rattus* lost contractability at reduced temperatures and *Rana* showed contractability to 0°C, but failed to respond to a stimulus upon rewarming until 10°C. All bat muscles tested continued to respond through all experimental temperatures, although the rigors of temperature stress greatly increased the duration of the twitches. The similarity of a bat muscle to a poikilothermic response can also be seen upon examination of twitch peak heights (Fig. 5). The duration of twitch, however, was considerably different from either the poikilotherm or homeotherm tested.

Henneman & Olson (1965) stated there is an inverse relationship between size and contractile acti-

vity of various muscles within the same species. They determined that this phenomenon was due to fiber orientation and fiber types, but hypothesize that the functional properties of the various motor units may be dependent upon the size of the motor neuron that innervates them. We have noted an apparent inverse relationship between muscle wt and force contraction in our study. We feel that fiber orientation and fiber type do not explain the relationship, since the same muscle was used for all species tested. The size of the motor neuron innervating the respective motor unit is a viable explanation and warrants further investigation.

Certain species of bats in the SW United States are actively flying throughout the year (O'Farrell *et al.*, 1967; O'Farrell & Bradley, 1970). In flight thermoregulatory responses of these bats in the winter is such that the animals are capable of coordinated motor activity at rectal temperatures near 20°C (Bradley & O'Farrell, 1969; Studier & O'Farrell, 1972; O'Farrell & Bradley, 1976). Recently, other body tissues have been examined and further show that flight muscles and brain are at similar low temperatures during coordinated motor activity (Hirshfeld & O'Farrell, 1976). It would seem reasonable to expect a correspondingly high degree of muscle function under these conditions, since these animals are active at reduced ambient and body temperatures (Figs 1, 2, 4 & 5). O'Farrell & Bradley (1976) report a difference in flight behavior during the winter, and the critical nature of these flights were for the maintenance of water balance rather than foraging. Instead

of slow, erratic insect pursuit, these animals used straight line, higher speed flight to and from watering holes. The adaptive significance of muscle response to ambient temperature is apparent. As temperature decreases, force contraction remains relatively constant, while twitch duration increases. This would promote straight line, higher speed flight, using fewer wing beats/unit time, thereby conserving energy expenditure.

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