

Contractile Function of a Flight Muscle Over the Range of Hibernation Temperature in Bats

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Studies on thermal adaptation postulate that optimal temperature of physiological properties matches a usually experienced body temperature (T_b) of organisms. Hibernating bats maintain T_b 's that are slightly higher than ambient temperatures (9°-12°C) of their wintering sites. To test the hypothesis that muscle function is adjusted to the T_b range of the hibernating animals, we examined contractile function of the *biceps brachii* muscle of Korean greater horseshoe bats, *Rhinolophus ferrumequinum korai* (n=5) at tissue temperatures between 10° and 35°C. Relative tetanic force (% of maximum force) was highest at temperatures of 10°-15°C, which match well their T_b 's during hibernation. Because non-hibernating endotherms with T_b of around 37°C show the optimal temperature for muscle force over 30°-40°C, our results strongly suggest that the flight muscle of the bats may exhibit thermal adjustments according to their seasonal T_b 's. The capacity to generate strong force at such low body temperatures may be adaptive, because bats must have muscles functioning to fly for occasional watering or excretion, or to move away from potential predators during hibernation.

KEY WORDS: Hibernation, Bat, Muscle Contractility, Flight Muscle, Temperature

Functional capacity of animals can be affected considerably by temperature. Since the environmental temperature fluctuates broadly over days and seasons, the effect of temperature could be even more significant for whose body temperature (T_b) changes according to the ambient temperature (Schmidt-Nielsen, 1990). If such poikilothermic animals have a fixed range of optimal temperature (T_o) where functional capacity is maximal, they would have problems of lowered fitness at temperatures outside the T_o range due to ineffective ecological performance (e. g., feeding activity, predator avoidance) (Huey and Stevenson, 1979). The theory on thermal adaptation has postulated that T_o matches a

usually experienced T_b of animals in order to maintain the best function. Thus, if an animal shows variable T_b 's according to ambient temperatures, the T_o would shift in parallel with the changing T_b . Previous studies on thermal dependence of muscle contractility and locomotion support this hypothesis. An example is seen in (altricial) red-winged blackbirds (*Agelaius phoeniceus*) (Choi and Bakken, 1990). Young blackbirds experience a broad T_b range (32°-42°C) for the first several days of hatching. They soon develop endothermic capability and can control T_b well in a high and narrow range (39°-43°C) after about a week of growth. For muscle contractility, 1-day blackbirds maintained 90% or higher of maximum tetanic force over tissue temperatures of 15°-40°C while 8-day (near-mature) chicks showed

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the force capacity decreasing rapidly at temperatures below 25°C. Further, T_o for feeding response (e.g., begging stretch) shifted ontogenetically from a range of 25°-40°C for hatchlings to a range of 40°-43°C for mature chicks (Choi and Bakken, 1990). Reptiles, amphibians, and many ectothermic species also show such adaptation for muscular and locomotory function to variable habitat temperatures (Brett *et al.*, 1958; Huey and Stevenson, 1979; Bennett, 1984; John-Alder and Bennett, 1987; Choi and Bakken, 1991).

Most species of bats in the temperate zone hibernate during winter. Because thermoregulatory cost would be high while food resources are scarce during the time (Schmidt-Nielsen, 1990), bats get into dormancy in their wintering sites until next favorable seasons. During the dormancy, bats are known to sustain T_b slightly above the ambient temperature (around 10°C). The animals are also believed to fly off the wintering sites briefly for watering or excretion several times during the period (Oh, 1993). These observations demonstrate that they normally experience low T_b 's during the hibernation period but, nevertheless, fly occasionally for the brief activities, probably at a condition of an increased T_b for that moment. In summer, bats are active and would have T_b of up to 40°C, similar to those of most non-hibernating mammals (manuscript in preparation). Thus, it is of much interest to examine how flight muscles of wintering bats function at their naturally experienced low T_b 's. We here report force production capacity at various temperatures of a flight muscle from hibernating Korean greater horseshoe bats, *Rhinolophus ferrumequinum korai*. We test a hypothesis that T_o for force production matches the T_b range over which the bats maintain in their wintering sites.

Materials and Methods

Animals

We captured bats hibernating in a deserted gold-mining cave located in Keyreong Mt., Korea. We measured cloacal temperature of the bats in place

and ambient temperature around the animals with a sensing tip of a 40 AWG copper-constantan thermocouple connected to an Omega HH-73T digital thermocouple thermometer. We carried several bats to our laboratory and kept them in dark, humid cages maintained at about 10°C. Body mass and cloacal temperature of individuals were measured before experiment.

In vivo isometric muscle contraction

Preparation. We anesthetized individual male bats with thiopental sodium (0.001 mg · g⁻¹ intraperitoneally) before dissection. Action of the anesthetic on the neuron, neuromuscular junction and muscle is known to be negligible (Price and Dripps, 1970). The long head portion of the *biceps brachii* muscle was isolated out and was soaked in the oxygenated cool Ringer solution in a petri dish. Tendons at both ends of the muscle were tied tightly with silk threads. The length of the tendons in the preparation was kept as short as possible in order to minimize tendon stretch at contraction. The muscle was placed horizontally in a muscle bath, where one end of the muscle was connected to a Grass FT-03 isometric force transducer, and the other end to an immovable holder. The muscle bath (size = 70 ml) was water-jacketed so that bath temperature was regulated within ± 1°C by circulating water from a refrigerated water circulator (Kookje Scien 33-WBF-15). Muscle temperature was measured with a sensing tip of the 40 AWG thermocouple dipped in the oxygenated Ringer solution and was read on the Omega HH-73T thermocouple thermometer. The Ringer composition (in mM) was: NaCl, 137; KCl, 5; CaCl₂, 2; MgSO₄, 1; NaH₂PO₄, 1; NaHCO₃, 24; glucose, 11 (at pH 7.35) (Faulkner *et al.*, 1982).

The muscle was stimulated by a pair of bright platinum electrodes connected to a Grass S48 stimulator that supplied a 1.0 msec square wave pulse or pulse train. All isometric signals were routed through a Grass 79 Polygraph, a Biopac MP100 A/D converter and then to an IBM AT compatible computer.

Procedure: In the beginning of each experiment, we established an optimum muscle length (l_o) and supramaximal stimulus strength where maximum

twitch tension was obtained. Once the l_o was set, the muscle was equilibrated until the tetanic force became constant over repeated contraction trials at the first test temperature. Contractile function was examined at 10°, 15°, 20°, 25°, 30°, and 35°C in each experiment. The temperature sequence was randomized in order to minimize the effect of time-based fatigue on contraction. At the end of experiment, we went back to the first test temperature and repeated a contraction trial at that temperature. We compared the force of the last trial to the first one (examined at the same temperature), and proceeded subsequent analyses with the data only when the difference between them was within 7%. The stimulus frequency at corresponding muscle temperatures in ascending order was 40, 70, 90, 120, 140, and 170Hz. We allowed a rest period of 20 min between stimulations.

After completion of each experiment, we froze the muscle in place (at l_o) with liquid nitrogen. We measured a cross-sectional area of the muscle to normalize tetanic force. The thickest middle portion of the muscle was thin-sectioned (8 μm) with a Microm HM 505E cryostat and was stained with a routine procedure of NADH diaphorase on slide mounts. Each image of the sections was scanned on a Scriptel RDT-1218 digitizer, and the largest area (Area_i) among those of several sections was taken for the normalization. Since the *brachii* muscle was bipinnate, this area should be adjusted by a factor of pinnation angle θ of the fibers radiated from the central tendon. To measure the pinnation angle, we obtained the *brachii* muscles from spare bats and froze them at l_o with liquid nitrogen. The muscle was thin-sectioned longitudinally for the central tendon being placed in the middle of the section. The sections were stained with safranin and methylene blue on slide mounts. The pinnation angles were measured on the Scriptel digitizer, and an average value was taken to adjust the cross-sectional area. The adjusted area (Area_{adj}) was calculated by a following equation:

$$\text{Area}_{\text{adj}} = \text{Area}_i / \cos\theta$$

Rate parameters of the isometric contraction were also determined from the force curves as

follows: tetanic rise time (TRT), a time period between 10% and 90% of peak tetanic force (F_o); the rate of tetanic force production (dF/dt), a slope of the curve between 10% F_o and 90% F_o ; and half relaxation time (HRT), a time period between a falling point of the curve and subsequent 50% F_o .

Data analysis

We here define an optimal temperature range for F_o or dF/dt as a range of muscle temperature where relative performance of the contractile properties was above 90% of the maximum performance over the experimental temperatures. Relative performance was computed by dividing the actual values by the absolute values of that individual at a standard experimental temperature. We defined the standard temperature as the temperature at which most individuals showed their maximal function. Significance of the effect of temperature on contractile properties was tested by oneway ANOVA at $\alpha < 0.05$ level, and general statistical tests were proceeded with SPSS/PC+.

Results

Body temperature during hibernation

Body temperature of the bats ranged between 9.3° and 12.8°C with a mean of 11.06°C \pm 1.23SD ($n = 8$) in January and February, 1995. The T_b of individuals was about 2°C higher than the ambient temperature (8°-11°C) around each animal. In April and May, the cave temperature remained almost the same that in the winter, but the T_b range of the bats broadened between 10° and 34°C as they became active in the warm season.

Isometric tetanic force

A typical curve of twitch and tetanic contraction examined at 10°C is shown in Figure 1. Absolute tetanic force (F_o) at each test temperature is given in Table 1, and relative tetanic force as a function of muscle temperature is presented in Figure 2. The relative forces were calculated using the absolute values given in Table 1 (see *Data analysis*

in Materials and Methods). Maximal F_o exerted by the *biceps brachii* muscle was 150.7 ± 28.8 mN. mm^{-2} (mean \pm SD, $n = 5$) occurring at 15°C . The effect of temperature on tetanic force generation was significant (oneway ANOVA, $P < 0.005$) in that the flight muscle showed a remarkable tolerance to cold but could not sustain a similar magnitude of force at muscle temperatures above 25°C . This resulted in an optimal temperature range of $10^\circ\text{--}25^\circ\text{C}$ for force production.

Time and rate parameters

Response time of the flight muscle during isometric contraction was reduced with increasing muscle temperature. As shown in Table 1, tetanic rise time (*TRT*) decreased from 424 msec at 10°C to 176 msec at 35°C , and half-relaxation time

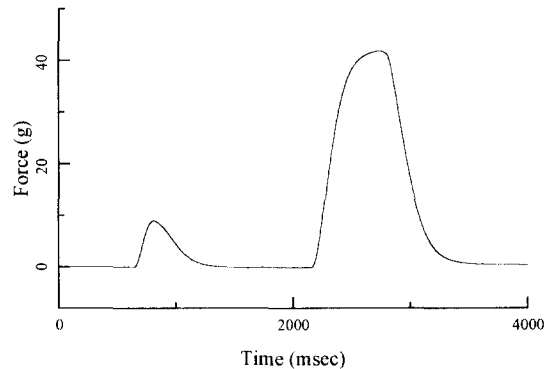


Fig. 1. A typical curve for twitch and tetanic contraction of the *biceps brachii* muscle from one Korean greater horseshoe bat, *Rhinolophus ferrumequinum korai*, examined at 10°C (body mass = 15.4g; cross-sectional area = 3.10 mm^2).

(*HRT*) decreased from 378 msec at 10°C to 150 msec at 35°C .

Absolute values of the rate of tetanic force production (dF/dt) ranged between 0.33 mN. $(\text{mm}^2.\text{msec})^{-1}$ at 10°C and 0.6 mN. $(\text{mm}^2.\text{msec})^{-1}$ at 25°C (Table 1). The dF/dt was affected by temperature significantly (oneway ANOVA, $P < 0.001$), with the curve rising steadily at temperatures up to 25°C and then falling afterwards (Table 1, Figure 3). Optimal temperature for dF/dt ranged between 25° and 30°C , and this range was $10^\circ\text{--}15^\circ\text{C}$ higher than that for the tetanic force. The upward shift in optimal temperature for dF/dt results from the relatively faster rate of reduction in *TRT* than the decreasing rate in F_o (Table 1) with increasing temperature; i.e., while F_o decreases by only 3.4% as the test temperature changes from 10° to 25°C , *TRT* decreases by 54.4% over that temperature change.

Discussion

Thermal adjustment of muscle performance

It has been questioned for more than a century that thermal adjustment on functional capacity occurs in most biological systems including biochemical to organismal levels (Brett *et al.*, 1958; Hochachka and Somero, 1984). Muscular and locomotory performance has also been thought to exhibit such adaptation according to an organism's thermal experience during its life history (Johnston *et al.*, 1975; Bennett, 1984). However, some studies argued that motor

Table 1. Isometric contractile properties of the *biceps brachii* muscle of Korean greater horseshoe bats, *Rhinolophus ferrumequinum korai*, as a function of muscle temperature.

| Contractile properties | Muscle temperature ($^\circ\text{C}$) | | | | | |
|------------------------|---|------------------|------------------|------------------|------------------|------------------|
| | 10 | 15 | 20 | 25 | 30 | 35 |
| F_o | 148.6 \pm 29.0 | 150.7 \pm 28.8 | 144.6 \pm 23.6 | 145.0 \pm 34.0 | 134.4 \pm 25.7 | 95.7 \pm 15.4 |
| <i>TRT</i> | 424.1 \pm 155.1 | 311.2 \pm 43.6 | 232.0 \pm 24.5 | 193.6 \pm 11.3 | 184.8 \pm 9.5 | 175.5 \pm 8.4 |
| <i>HRT</i> | 378.4 \pm 85.8 | 373.2 \pm 79.8 | 290.8 \pm 79.1 | 288.8 \pm 31.1 | 204.0 \pm 76.4 | 150.0 \pm 49.0 |
| dF/dt | 0.33 \pm 0.19 | 0.386 \pm 0.03 | 0.50 \pm 0.06 | 0.60 \pm 0.12 | 0.58 \pm 0.1 | 0.47 \pm 0.14 |

Data in mean \pm SD; $n = 5$.

Units are: F_o in mN. mm^{-2} , *TRT* and *HRT* in msec; dF/dt in mN. $(\text{mm}^2.\text{msec})^{-1}$.

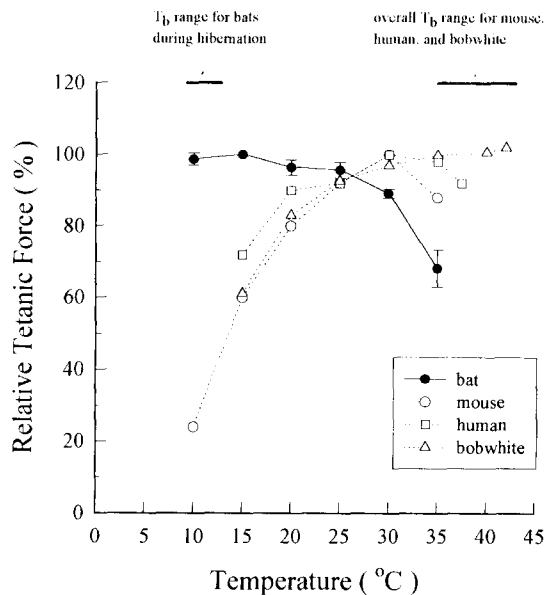


Fig. 2. Relative tetanic force of the flight muscle in bats (dark circle) as a function of muscle temperature. All points are means, and the vertical bars represent ± 1 SD ($n = 5$). Shape and position of the relative force curve for the bats were compared with those for mouse (open circle, Lannergren and Westerblad, 1987), human (open square, Ranatunga *et al.*, 1987), and northern bobwhite (open triangle, Choi and Bakken, 1991). Dark horizontal bars shown at the top x-axis are the range of core T_b of each species.

functions do not fully follow the general observation of thermal adjustments (i.e., acclimation) (Renaud and Stevens, 1981; Rome, 1983).

Our findings on the relationship between T_o for force generation and T_b of the hibernating bats strongly support the basis of thermal adjustment in muscle contractile function. Force generation capacity in the bats was highest at tissue temperatures between 10° and 15°C, and this range matched well the T_b range (9°-13°C) of the animal during hibernation (Figure 2). This observation is in fact quite amazing, because the curve shape for our bats was almost opposite to those for non-hibernating mammals and birds examined (Figure 2). T_o the latter cases, tetanic force is maximum over the tissue temperature of 35°-43°C and decreases rapidly at temperatures below 20°-25°C. The T_o range for the force

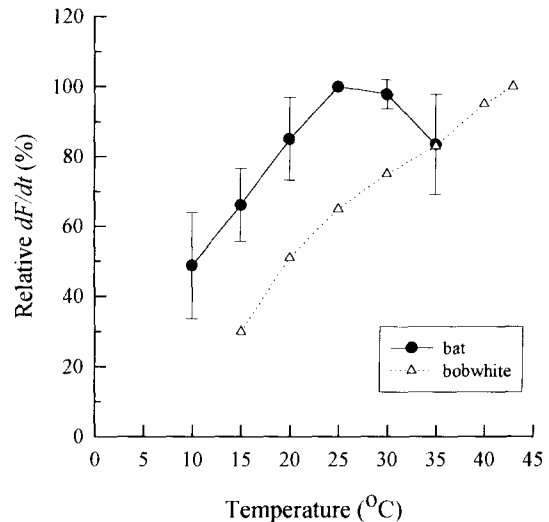


Fig. 3. Relative rate of tetanic force production (dF/dt) in bats (dark circle) as a function of muscle temperature. All points are means, and the vertical bars represent ± 1 SD ($n = 5$). Shape and position of the curve for the bats were compared with those of northern bobwhite (open triangle, Choi and Bakken, 1991).

production in the non-hibernating endotherms therefore matched well the T_b range of 35°-43°C in these animals (Figure 2).

Our finding of the T_o range for contraction rate (25°-30°C) provides another support for thermal adjustment of the flight muscle. As illustrated in Figure 3, the curve pattern of the bats differed from that of northern bobwhites in that the curve was positioned 10° to 15°C lower than that for northern bobwhites over the experimental temperatures, while the curve for the latter was rising constantly with temperatures up to 43°C. We suspect that the T_o range of dF/dt for bats would be associated with the lowest T_b at which the animals initiate flight trials for watering or excretion during hibernation. Simoizumi's study (Woon, 1967) and our observation (manuscript in preparation) suggest that the bats could practise flight at T_b as low as 28°-32°C.

Contractile performance compared to other studies

A direct comparison of our study among other species of bats is not readily feasible since thermal dependence of tetanic contraction had scarcely

been examined previously for these animals during hibernation. In mammals (mouse, rat, rabbit, guinea pig), the maximal tetanic force of various muscles ranges between 132-212 mN.mm⁻² (Josephson, 1993). The flight muscle of bats produced the maximal force of 150.7 mN.mm⁻², which is positioned at a lower side of the force range of the mammalian muscle. It is probable that the flight muscle of the bats during hibernation is not likely to generate so strong force as does the muscle during active seasons, since constituents in the muscle fibers such as contractile proteins and activity of catalytic enzymes (e.g., pyruvate kinase, phosphofructokinase) are known to decrease significantly during hibernation (Yacoe, 1983; Hachimi *et al.*, 1990).

The dF/dt (the straight slope in the tetanic rise phase) of the bats (Table 1) appeared to be relatively low, compared to other cases. The soleus (slow-twitch) and flexor digitorum longus (fast-twitch) of cats show 0.65 and 0.87 mN.(mm².msec)⁻¹, respectively, at 27°C (Buller *et al.*, 1984). The gastrocnemius muscle from near-mature chicks of northern bobwhites and red-winged blackbirds developed the contraction rate of 1.02-1.05 mN.(mm².msec)⁻¹ at 25°C (Choi and Bakken, 1991). The highest dF/dt occurring at 40°C is 1.0 mN.(mm².msec)⁻¹ in cat and 1.5-1.6 mN.(mm².msec)⁻¹ in the two bird groups. Time variables (*TRT*, *HRT*) are not easily comparable with other data because of the difference in definition as well as few studies on muscle contractile function in bat species.

Conclusively, the flight muscle of our bats has a relatively low force generation capacity and slow tetanic response (e.g., dF/dt , *TRT*) over the hibernation T_b range compared to other mammalian species.

Further questions

A question raised from this study is *how* the muscle can produce maximum force at low temperatures. From biochemical perspectives, it may be probable for muscle fibers to produce isoforms of contractile proteins and enzymes (e.g., myosin, ATPase, etc.) according to seasonal T_b 's of the bats (see Hochachka and Somero, 1984;

Hachimi *et al.*, 1990). In other words, 'winter' isoforms of which activity (in terms of affinity to their substrates) is highest at the low temperature would be expressed in the muscle fibers during hibernation. 'Summer' isoforms that are most active at higher temperatures would be expressed as well in warm seasons, for the bats exhibit T_b between 10° and 34°C during the seasons. As experimental evidences (Hochachka and Somero, 1984) point out, ectotherms like barracuda and fish experiencing a wide fluctuation of T_b have multiple locus isoenzymes (e.g., lactate dehydrogenase, acetylcholinesterase) which function over the broad T_b range, whereas those experiencing a narrow T_b range in other habitats have a single (or limited) locus enzyme associated with motor function.

The other question followed is *why* the T_o range is low in the bats during hibernation. If the bats have T_b of up to 35°-40°C during the active period of the year, can't we simply anticipate that the T_o range in the bats remains at the high T_b range during active seasons, like in non-hibernating endotherms, while the T_o range is expanded downward to the hibernation T_b range during winter? Several answers to this question would be: *First*, as described above, biochemical adjustment may be so directed for the contractile isoforms to be most active at the low temperatures. The contractile system will be of no efficiency energetically if the muscle functions well at all temperatures including the range above 25° C over which the animals barely experience during hibernation. *Second*, the capacity to generate the greatest force in the low range of T_b may be crucial for survival, because this capacity would provide a defence mechanism for the animals against potential predators (even if predation risk may be low for the period). The bats may be able to move away from predators or even to bite them with strong muscle force at such low temperatures. This type of behavioral response at low temperatures is observed in other animals like agamid lizards. According to Hertz *et al.* (1982), the lizards in their T_o range (35°-40°C) normally ran away from large-sized predators when they were able to out-run the predators. However, when their T_b was lower than the T_o , they dared

to attack back and to bite the predators. This behavioral change of the prey from flight at a warm T_b to fight at a cool T_b seems to reflect contractile capacity of their skeletal muscle. For instance, the animal has tetanic force decreased by only 20% when the tissue temperature was lowered from 35° to 20°C, whereas it suffers reduction of muscle shortening velocity by 63% with the same degrees of thermal decrease (Marsh and Bennett, 1985). Third, the force generation capacity at the low T_b 's may facilitate thermogenesis of the bats through the shivering mechanism, although non-shivering thermogenesis (e.g., brown fat burning) may prevail total heat production (Schmidt-Nielsen, 1990). Because the bats can not fly around for excretion or watering at the low hibernation T_b , they should increase T_b to some degrees (e.g., up to 28°C) for a brief period of time. The most effective and fast way of increasing T_b is known to be the non-shivering thermogenesis (Schmidt-Nielsen, 1990), but if shivering of the skeletal muscles is joined in the process, the overall thermogenesis will be more accelerated. These hypotheses however require further test in the future.

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박쥐의 동면온도 범위에서 작용하는 비행근의 수축기능

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온도 적응에 관한 연구들을 보면 생리기능 상의 최적온도가 생물 개체의 일상 체온에 잘 일치한다는 내용을 보여주고 있다. 동면 중의 박쥐들은 월동장소의 주위온도(9°-12°C)보다 약간 높은 범위에서 체온을 유지하는 것으로 관찰되고 있다. 본 연구에서는 이 동물들의 근육이 동면체온 범위에서 최대의 수축기능을 발휘하도록 조정되리라는 가설을 설정하고 이를 시험하기 위해 한국큰관박쥐 *Rhinolophus ferrumequinum korai*(n = 5)의 이두박근 수축기능을 10°-35°C 범위의 근육온도에서 실험하였다. 상대적 강축힘(최대 강축힘에 대한 퍼센트 값)은 이들의 동면체온과 일치하는 10°-15°C 범위에서 가장 높았다. 한편 비동면성 동물은 37°C의 범주에서 체온을 유지하며 강축힘에 대해 30°-40°C 범위의 최적온도를 보이는데 이를 종합해 볼 때 본 연구의 결과는 박쥐의 비행근 기능이 계절적인 체온변화에 준하여 조정되고 있음을 보여준다고 하겠다. 박쥐의 근육이 낮은 체온에서도 강한힘을 발생한다는 본 실험결과는 동면동안 이따금 수분섭취나 배설을 위해 날아야하는 점 또는 천적으로부터 도피할 수 있어야 하는 점을 고려할 때 적응의 한 예라고 사료된다.