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SEQUENTIAL CHANGES IN REGIONAL DISTRIBUTION OF BLOOD IN *EPTESICUS FUSCUS* (BIG BROWN BAT) DURING AROUSAL FROM HIBERNATION

by

© JOSEFINE CONSTANTIA RAUCH

A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Sequential changes in regional distribution of blood in *Eptesicus fuscus* (big brown bat) during arousal from hibernation" submitted by Josefine Constantia Rauch, in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

The sequence of changes in the regional distribution of blood was determined in arousing big brown bats by measuring the regional uptake of injected 86-Rubidium (Sapirstein, 1958) in groups of bats at close, successive intervals during the arousal from hibernation (T_a = 5 C) in the winter and in the summer. The distribution of blood was also determined in deeply hibernating bats (T_a = 5 C) and in post-arousal bats (T_a = 22 C) during the winter and summer, and in anaesthetized, non-hibernating bats (T_a = 22 C) during the summer. Heart rates were measured under similar conditions and blood flow rates approximated by assuming a constant average stroke volume of 0.024 ml.

In bats hibernating during the winter, the fraction of cardiac output received by the majority of organs approximated the fraction of the body weight contributed by these organs. Important exceptions were the myocardium, which received a relatively high fraction, and the skin, which received a relatively low fraction of the cardiac output.

Following the initiation of arousal from hibernation in the winter, there was a progressive decline in the fractions of the cardiac output going to organs of the posterior body, and a progressive rise in the fractions going to organs of the anterior body. The relative fraction of the cardiac output delivered to brown adipose tissue rose more rapidly and at an earlier time during arousal than did those delivered to other tissues. During the second half of the arousal process the reverse occurred. It started with a decline in the fractions of the cardiac

output going to brown adipose tissue and a gradual rise in those to posterior body regions. Similarly, capillary blood flow rates in anterior body regions increased rapidly during early arousal whereas those in posterior body regions did not rise markedly until late arousal. A different requirement for oxygen by brown adipose tissue as compared to other tissues and the comparatively high heat production by brown fat are believed to be major factors in determining the redistribution of blood in arousing big brown bats.

The regional distribution of blood in post-arousal bats in the winter was not grossly different from that in their deeply hibernating counterparts. However, the estimated cardiac output and consequently capillary organ blood flow rates were about forty times higher in post-arousal bats than in hibernating bats. This suggests that the major changes in circulation between the two groups of bats are primarily due to differences in blood flow rates.

The fractions of cardiac output delivered to the skin, myocardium, kidneys and other organs were higher in bats subjected to cold (T_a = 5 C) in the summer than in those under similar conditions (deep hibernation) in the winter. Bats that were capable of arousing in the cold during the summer had considerably higher fractions of the cardiac output going to the skin (and other organs) and significantly lower fractions going to brown adipose tissue than did their winter counterparts. The estimated blood flow values to these organs showed similar trends. The mortality rate was high in bats subjected to cold in the summer. Also, many of the bats that did survive in the cold for one or two weeks failed to raise their heart rates above 120 to 180 beats per minute during the arousal.

They were considered incapable of arousing in the cold. The findings indicate that there are obvious limitations in circulatory adjustments in bats subjected to cold during the summer.

The distribution of blood in non-hibernating, anaesthetized bats differed from those of deeply hibernating and post-arousal bats. Most pronounced was the comparatively high fraction of the cardiac output received by the skin and the low fraction received by the anterior muscles of anaesthetized bats. These findings are probably associated with Sodium Pentobarbital anaesthesia.

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INTRODUCTION

The single, most important parameter in the arousal from mammalian hibernation is a profound change in the metabolic state of the organism. This change, which involves a "maximum amount of heat production within a minimum amount of time" (Lyman and Chatfield, 1955), can be explained satisfactorily only in terms of rapidly accelerating and progressively shifting biochemical and physiological processes.

Most extensive studies documenting physiological changes in arousing hibernators have involved direct measurements of body temperatures. Not only is there an increase in temperature during arousal, but a more rapid warming of anterior body regions has been found. Dubois (1896) first demonstrated differential warming during the arousal from hibernation in the European marmot, *Arctomys (Marmota) marmota*. He recorded temperatures (highest to lowest) in the order of: oesophagus, pectoral muscles, liver, mouth, thigh, and rectum. Other investigators have obtained similar results in the European marmot (Pembrey, 1901); thirteen-lined ground squirrel, *Citellus tridecemlineatus* (Johnson, 1929; Adolph and Richmond, 1955); Syrian hamster, *Mesocricetus auratus waterhousi* (Lyman and Chatfield, 1950); and in the golden hamster, *Mesocricetus auratus* (Adolph and Richmond, 1955). In all hibernators investigated, a temperature gradient between anterior and posterior body regions has been found to develop during arousal (review: Lyman, 1965). This was interpreted as a consequence of a posterior vasoconstriction, which reduces the "amount of heat lost from the body surface" and

consequently the time during arousal.

Such data on regional body temperatures (and other parameters) have been utilized frequently in the attempt to discern which organs and tissues are of particular importance as sites of heat production during the arousal from hibernation. Early investigators argued that the primary source of heat is the liver (Dubois, 1896), skeletal musculature (Pembrey, 1901), or "some source within the thorax" (Johnson, 1929). Evisceration experiments (Lyman and Chatfield, 1950) indicated that none of the abdominal organs contributed significant amounts of heat to the overall thermogenesis during arousal; the eviscerated hamsters aroused almost as quickly as the non-eviscerated ones. In contrast, inhibition of shivering thermogenesis by curarization retarded the warming process considerably. These investigators obtained evidence of a direct relationship between heart rate and body temperature increments in intact hamsters during arousal at an ambient temperature (T_a) of 5 ± 2 C. In eviscerated, curarized hamsters, arousing under similar conditions, heart rates became maximal and body temperatures rose to about 27 C in contrast to 37 C attained by control animals. The ability to attain a relatively high body temperature, in spite of impaired shivering thermogenesis, led the authors to conclude that the heart, next to skeletal muscles, is the most important site of heat production during arousal. This seems unlikely, however, because of the relatively small size of the heart as compared to the total mass of the body. More recent evidence (reviews: Smith and Horwitz, 1969; Lindberg, 1970) makes it apparent that the heat production by the animal's brown fat must have contributed greatly to the temperature increments in the curarized hamsters used by Lyman and Chatfield.

During the last decade, considerable evidence has been obtained which confirms that brown adipose tissue has an important thermogenic function in a variety of mammals (reviews: Smith and Horwitz, 1969; Lindberg, 1970), and that its maximal thermogenesis is evoked during the arousal from hibernation (Hayward and Lyman, 1967). This has been demonstrated first by Smith and Hock (1963), who recorded higher temperatures from the axillary brown fat area than from other subcutaneous body regions of the arousing yellow bellied marmot, *Marmota flaviventris*; also, a maximum temperature difference of about 13 C was recorded between the axillary brown fat and the rectum during the arousal process. Because brown adipose tissue was observed mainly in the thoracic region, they considered that a close relationship must exist between this tissue and major blood vessels of the anterior body (Hammar, 1895; Smith and Roberts, 1964; Rauch and Hayward, 1969) to enable transfer of heat to the blood in these vessels. Thus, although the relative mass of brown fat was small, heat could be transferred conveniently to the "cardiorespiratory" organs, spinal cord and nerves. Subsequent workers showed that the temperature of brown adipose tissue exceeded that of the heart in the arousing big brown bat, *Eptesicus fuscus* (Smalley and Dryer, 1963; Hayward *et al.*, 1965), and in the European hedgehog, *Erinaceus europaeus* (Edwards and Munday, 1969). Opposing results were obtained for the awakening woodchuck, *Marmota monax*; the door mouse, *Glis glis*; and for the golden hamster (Lyman and Taylor, 1964). Axillary brown fat had a slightly lower temperature than aortic blood in the golden-mantled ground squirrel, *Citellus lateralis*, during the first two-thirds of the arousal process (Hayward *et al.*, 1965). The rise in brown fat temperature above that of

the "heart" during the final phase coincided with a rapid warming of caudal areas. This suggested, but did not prove, a "sudden increase in the circulation" to the posterior body.

Experimental studies have resulted in a wealth of histochemical and biochemical data related to the thermogenic capability of brown adipose tissue in general (reviews: Smalley and Dryer, 1967; Smith and Horwitz, 1969; Lindberg, 1970). However, relatively few of these studies concerned brown fat during the arousal process. A decline in the tissue's glycogen and lactate content, and a rise in its pyruvate level in the arousing thirteen-lined ground squirrel has been reported by Zimny and Gregory (1958). Konttinen *et al.* (1964) found a significantly higher free fatty acid concentration in brown fat deposits of hibernating and arousing European hedgehogs than in active animals. The ATP (adenosine triphosphate) concentration in the brown adipose tissue of bats (*E. fuscus*) was high in hibernation and declined by a significant amount during the arousal (Dryer and Paulsrud, 1966). Subsequent studies indicated a disappearance of fat vacuoles and a decrease in brown fat triglycerides in arousing golden-mantled ground squirrels (Spencer *et al.*, 1966) but not in golden hamsters (Feist and Quay, 1969). *In vivo* oxygen tensions and oxidation-reduction states of pyridine nucleotides were determined for brown adipose tissue in non-hibernating and arousing golden hamsters (Prusiner *et al.*, 1968). Quantitatively similar oxidation-reduction states occurred at a lower oxygen tension in arousing hamsters. Furthermore, the infusion of norepinephrine caused a fall in the tissue's oxygen tension, a reduction in fluorescence of the mitochondrial NAD^+ (nicotinamide adenosine dinucleotide) system, and a rise in brown fat

temperature. The authors concluded that brown fat is in a "higher metabolic state" in arousing than in non-hibernating hamsters. They suggested that the tissue's "heat production is controlled by the rate of (cellular) respiration" and that "triglycerides, through the mediation of norepinephrine, provide the respiratory fuel."

The reduced rate of incorporation into tissue protein of l-histidine-2,5-^{3}H at low temperatures provided evidence of a decreased protein synthesis in brown adipose tissue and other important organs in the arousing mouse-eared bat, *Myotis myotis* Borkh. (Heldmaier, 1969). The logarithm of incorporated histidine, plotted against various temperatures during arousal, gave straight line relationships. Because statistically significant differences between the regression equations of these lines could not be detected, Heldmaier concluded that protein synthesis in brown adipose tissue (and in other organs investigated) is not related to the thermogenic activity of this tissue during arousal.

Finally, brown fat homogenates from hibernating (T_a = 5 C) big brown bats have a greater capability to oxidize certain substrates and do so with a greater "thermal efficiency" than brown fat homogenates from cold-acclimated (T_a = 5 C) albino rats, *Rattus norvegicus* (Dryer *et al.*, 1970). These investigators studied the oxidation of labelled palmitic, oleic, and succinic acids at 5-degree intervals between 5 C and 37 C, and found that, at all temperatures, the amount of CO_2 liberated from palmitate and oleate was greater for the tissue preparations from the bat than for those of the rat. Below 30 C, the amount of CO_2 obtained from succinate was greater for the preparations from the bat; above 30 C it was greater for the preparations from the rat. Furthermore, below

this temperature, the calculated E_a (energy of activation) for all oxidation processes studied was lower in the brown fat homogenates from bats and this comparatively low energy requirement is presumably associated with the ability to arouse from hibernation.

Such dynamic adjustments as occur in arousing hibernators implicate parallel changes in circulatory parameters. Both enhanced metabolism and differential warming must depend upon (or be a consequence of) the disposition of the circulating blood. This view has been expressed before (Lyman, 1965); however, data which attest a sequence of necessary circulatory changes during the course of arousal are still wanting. The distribution of blood has apparently not been demonstrated for any species in deep hibernation, although Bullard and Funkhauser (1962) purport to have done so. However, the relatively high heart rates of their experimental animals suggest the phase they denoted as deep hibernation was in reality early arousal.

To demonstrate the distribution of blood in arousing hibernators, early investigators injected the dye indigo carmine into the jugular vein and observed its distribution. Mares (1892) injected it into the European ground squirrel, *Spermophilus citellus (Citellus citellus)* and Dubois (1896) into the European marmot. The dye appeared first in the regions of the head, thorax, forelimbs, and much later in posterior body regions. It did not freely enter the capillaries supplying the viscera (Dubois, 1896). A subsequent, angioradiographic study of the Syrian hamster by Lyman and Chatfield (1950) strengthened the conclusion that blood flow to posterior body regions is delayed in arousing hibernators. Recently, it has been substantiated that, at least during mid-arousal,

the distribution of blood is such as to denote enhanced capillary (nutritional) blood flow to the myocardium, anterior skeletal muscles, and brown adipose tissue in the Arctic ground squirrel, *Spermophilus (Citellus) undulatus* (Johansen, 1961), and in the little brown bat, *Myotis lucifugus* (Rauch and Hayward, 1970). On estimating regional blood flow by 86-Rb (rubidium) distribution during three stages (heart rates 25, 100, 200 beats/minute), Bullard and Funkhauser (1962) found a similar dispersion of blood in the thirteen-lined ground squirrel.

Estimated rates of heat production and heat loss, as measured by oxygen consumption and total body calorimetry, have provided indirect information regarding circulatory adjustments in hibernating and in arousing thirteen-lined ground squirrels (Hammel *et al.*, 1968). The rate of heat production, which equalled the rate of heat loss, was found to have a normal temperature coefficient (Q_{10} = 2.39) over a relatively wide range of hibernating temperatures (T_a = 3 C to 13 C), and the temperature difference between the hypothalamic temperature and the air temperature was shown to be a function of the air temperature. This indicated that tissue temperatures and activation energies of metabolic processes rather than centrally controlled thermoregulatory responses determine the metabolic rate during deep hibernation, and that peripheral vasomotor tone remains unaltered during this physiological state. These workers also maintained that a reactivated thermoregulatory system during arousal would explain vasoconstriction to posterior body regions (Lyman, 1948; Lyman and O'Brien, 1960; Johansen, 1961; Bullard and Funkhauser, 1962), and consequently, the rapid rise in hypothalamic temperature during early arousal (Hammel *et al.*, 1968). Furthermore, the decline in hypothalamic

temperature increments during late arousal was interpreted as a consequence of vasodilatation in posterior body regions.

The overall pattern of circulatory adjustments in individual hibernators would best be indicated by a continuous blood flow or blood distribution study, to be made during deep hibernation and during the entire course of arousal. Unfortunately, this is not feasible because many technical difficulties would have to be overcome. The use of indicators, such as radioactive substances, involves the killing of the animal at a given time after equilibrium has been established between the indicator and its exchangeable substance (Sapirstein, 1958). Therefore, the distribution of blood in any one animal can only be measured at one given point in arousal. If one measures the distribution of blood in groups of individuals, at close, successive stages during arousal, one can reconstruct the events that reflect those in an individual animal over the entire period of the arousal process. Such an approach has its limitations, but if experimental errors are minimized, variations obtained from "point" measurements will fall within the normal distribution range, similar to continuous measurements.

Knowledge of the sequence of changes in the distribution or flow of blood during arousal provides a means of evaluating hypotheses regarding circulatory adjustments (Lyman, 1965; Hammel, 1968). The present study will reveal any fluctuations in blood flow to given body regions and it will indicate whether or not enhanced blood flow to certain organs or tissues involves decreased flow to others. Furthermore, data on nutritional blood flow to metabolically active organs will provide the basis for quantitative measurements of heat production by such tissues.

On these premises, the present study was undertaken to solve some of these problems and to serve as a reference for further investigations.

The big brown bat, *Eptesicus fuscus*, was selected for this study because it could be obtained in sufficient numbers to provide relatively large sample sizes. Furthermore, the animals are large enough to permit cannulation of certain blood vessels, while not too large to count radioactivity of entire organs following the injection of an isotope. *Eptesicus fuscus* is a predictable hibernator, and hemodynamic parameters have not been investigated in this species.

MATERIALS AND METHODS

The species (*Eptesicus fuscus* Beauvois) investigated was identified using the key of Babour and Davies (1969). Animals were of both sexes and adults, that is, they had hibernated for at least one winter in their own habitat. Experiments were carried out in the Department of Zoology, University of Alberta, Edmonton, between May 1969 and February 1971.

A. SOURCE OF BATS

Approximately 50 bats were removed by hand from a cave near St. Paul (45° 00' N; 93° 07' W), Minnesota, in late February, 1970. They were placed in wiremesh cages and transported by air to Edmonton (53° 30' N; 113° 45' W), Alberta.

All other bats used in this study were collected locally from farm houses near Morinville (53° 14'N; 113° 45' W) and Rollyview (53° 14' N; 113° 20' W), in July, 1969, and near Leduc (53° 14' N; 113° 30' W), in August, 1970. They were captured with mist nets set up in front of bat exit holes under the eaves of houses. Upon leaving their daytime roosting places, large numbers of bats flew into the nets. Animals so captured were cut free of the net, placed in wiremesh cages, and taken to the University.

B. CARE OF BATS

1. Non-hibernating Bats

Two to four individuals were housed in large wiremesh cages. To

ensure a relatively high humidity, the cages were covered with moistened towels. Once a day, usually in the evenings, bats were removed and given food individually in small feeding chambers. These consisted of Plexiglass walls (10 x 10 x 3 cm) and a snaptop wiremesh lid. Petri dishes with food, semi-lean ground beef and meal worms (*Tenebrio* sp.), were placed inside the chambers next to bats. Animals developed the new feeding habit within two weeks of capture. Cow's milk and small amounts of a vitamin mixture (Poly-Vi-Sol)[1] was given twice a week, and water was supplied *ad libitum*. In addition to feeding bats individually, which ensured that all obtained food, a large dish of ground beef was placed into each cage late in the evening.

All bats were kept at room temperature (T_a = 22 C) for a minimum of three months prior to experimentation. During this time, mortality was less than 2 percent.

2. Hibernating Bats

Bats were placed individually into plastic mouse cages, previously furnished with Underpads.[2] These pads, composed of a plastic sheet and several layers of compressed cotton, extended loosely over the inner sides of the cages and were held in position by the wiremesh lid. Bats could either hang up on the pads or hide behind them. Possible dessication of animals was prevented by moistening the compressed cotton and placing wet towels on the lids. These were covered, in turn, with plastic sheets so as to leave a narrow space at either end for air to

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[1]Mead Johnson Laboratories, Canada Ltd., Toronto, Canada.

[2]Johnson and Johnson Ltd., Montreal and Toronto, Canada.

circulate freely. The animals had free access to water but food was not supplied. Cages were situated behind wooden boards in a dark environmental chamber[3] at an ambient temperature of 4 to 5 C.

Bats placed into the cold during the winter were allowed to hibernate for 3 to 6 weeks before being used in this study. To determine whether the animals were healthy and the conditions were appropriate for hibernation, three animals were chosen at random and allowed to hibernate from early November to early March. None of these animals died.

Bats subjected to cold during the summer were kept in hibernation for 1 to 2 weeks prior to experimentation. This shorter time interval seemed preferable because of the high mortality of bats placed into the cold in summer. A positive correlation was noticed between death rate and time in cold. Furthermore, mortality increased between early June and late July, when most of the animals died within two weeks. After the end of August, death rate declined. Increasing the cold-room (environmental chamber) temperature to 10 C did not reduce mortality.

C. PROCEDURES

1. Anaesthesia

Anaesthesia was required for the blood distribution study of non-hibernating bats and for the implantation of electrocardiogram (EKG) electrodes. Pentobarbital Sodium, injected intraperitoneally, was required in doses of 40 to 60 mg per kg of body weight in the summer, and 60 to 80 mg per kg of body weight in the winter. The anaesthetic became

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[3]Foster, Drummondville, Quebec, Canada.

effective within 15 minutes provided no handling occurred during this time. All anaesthetized animals survived. Recovery time was less than 1 hour at ambient temperatures above 23 C, and more than 3 hours at a temperature of about 20 C.

2. Heart Rate

The standardization of intervals during arousal at which blood distribution measurements were made requires a knowledge of possible heart rate changes in arousing bats. Therefore, heart rates were measured during arousal in:

1. 20 bats arousing in winter
2. 30 bats arousing in summer

Additional heart rate measurements included:

3. 8 bats deeply hibernating in winter
4. 8 bats deeply hibernating in summer
5. 10 bats non-hibernating, anaesthetized
6. 10 bats non-hibernating, non-anaesthetized

A Sanborn polygraph (Model 7714-09 A) was utilized for recording electrocardiograms (EKG's) and consequently, for obtaining heart rates. These were determined by counting the number of heart beats within a 150 mm section on the chart paper of the inbuilt chart recorder. Since the speed with which the paper moved was known, the average heart rate at a given time during arousal could be calculated. Two methods were employed:

Method 1. Electrodes consisted of plastic tubing (length = 3 mm; internal diameter = 2 mm) with a pinhole in the center of one side, and a piece of nickel-chrome wire (size = 0.1 mm) extending via the pinhole into

and through the lumen. Several turns of wire, wound over the outside and through the lumen, provided a narrow space for the acceptance of needle connectors. The free end of the wire, protruding through the pinhole, was bent back on itself to form a smooth tip which could be implanted permanently into the animal.

Three electrodes were implanted in each bat. The sites chosen were an area dorsal to each acromion process and dorsal to the left transverse process of the first or second lumbar vertebra.

The animals were anaesthetized and a small incision made into the skin. The tip of the electrode connector was forced through the incision and stitched under with surgical thread. Bats were allowed to recover at room temperature (20 to 23 C) for a minimum of 5 days and then placed in the cold room (4 to 5 C).

After the animals had been in hibernation for a minimum of 8 days heart rates were measured during arousal. The experiments were performed in the cold room at an ambient temperature of about 5 C. Bats were removed from their cages and placed on a table, previously covered by a towel. This prevented animals from sliding over the smooth surface of the table. Needle connectors were inserted into the implanted electrodes, and leads were anchored to prevent a pull on the animal. The leads were then connected to the polygraph situated outside the cold room. In most experiments, heart rates were recorded every two minutes during arousal. In four summer experiments and in four winter experiments, continuous records were made. From these measurements curves were constructed for heart rate versus time during arousal.

When measuring heart rates in deep hibernation, bats were not

removed from their cages. Leads were taped to the outside of the cage, previously located in a readily accessible area. Upon removing the lid of the cage, the implanted electrode was gripped carefully with forceps, and the needle connector inserted into it. Subsequently, the lid was replaced again. Heart rates were recorded immediately and at intervals within the following 48 hours. Relatively few experiments were successful since the slightest disturbance caused arousal of bats, particularly in winter.

Method 2. Needle electrodes were inserted directly under the skin in the areas described before. This was less time-consuming and did not require anaesthesia, but it evoked arousal and hence could not be used in hibernating bats.

3. Blood Distribution Study

1. Principle. The method used was essentially that of Sapirstein (1958). A given amount of radioactive rubidium (86-Rb) is injected intravenously and allowed to circulate for a given period of time (30 to 60 seconds in non-hibernating mammals). The animal is then killed rapidly, its tissues excised, and assayed for radioactivity. Knowing the amount of rubidium injected and the amount taken up by various organs, the fraction of cardiac output delivered to these organs can be calculated.

The validity of the technique depends upon the criteria that all tissues, except the brain, show similar extraction ratios for the isotope (Sapirstein, 1958), and that 86-Rb is a flow-limited substance (Friedman, 1968). It is extracted effectively across capillary beds but not across arterio-venous shunt systems (Friedman, 1971). Low body temperatures, as

occur in hibernating mammals, have no detectable effect on the uptake of the isotope (Bullard and Funkhauser, 1962).

2. Grouping of animals. For blood distribution studies, bats were grouped as follows:

Group A: Non-hibernating bats. This group consisted of 10 individuals, 5 from Alberta and 5 from Minnesota. The animals were anaesthetized prior to experimentation, carried out in the summer at an ambient temperature of about 22 C.

Group B: Hibernating and arousing bats (winter experiments). This group of 94 bats from Alberta consisted of 11 subgroups of 8 individuals and 1 subgroup of 6 individuals. The experiments were performed in the cold-room (T_a = 5 C) during the winter.

Group C: Hibernating and arousing bats (summer experiments). This group of 49 individuals, 20 from Alberta and 29 from Minnesota, consisted of 11 subgroups of 4 to 5 animals. The experiments were performed in the cold-room (T_a = 5 C) during the summer.

Eighteen bats from Alberta and 16 bats from Minnesota (not denoted as a distinct group) were used in preliminary arousal studies, designed to ascertain that low body temperatures have no detectable effect on the uptake of 86-Rb and to establish an appropriate interval between isotope injection and killing of the animal by KCl injection.

3. Isotope: preparation and injection. A fixed amount (0.6 millicuries) of radioactive rubidium, purchased[4] in the form of 86-RbCl in 1 N HCl and in concentrations of 2.0 millicuries (mc) per ml, was

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[4]New England Nuclear, 575 Albany Street, Boston, Mass., U.S.A.

evaporated to dryness and redissolved in 0.6 ml of mammalian saline. Prior to injection, 0.05 ml of this solution was diluted further such that 0.025 ml, the amount injected, contained about 1 microcurie (μc) of 86-Rb.

When solutions of 86-RbCl in 1 N HCl were not evaporated and redissolved in saline, bats responded to injection by emitting squeaks and making sudden movements.

The cannula used for injecting the isotope consisted of 4 cm of PE 10 polyethylene tubing into one end of which was inserted a 30 gauge hypodermic needle without a luer lock hub. A Tuohy-Borst Adapter,[5] attached to the other end of the tubing, accommodated a hypodermic syringe. The cannula assembly was filled with heparinized mammalian saline to remove air and prevent clotting of blood.

Non-hibernating, lightly anaesthetized bats were placed on a pad under a dissecting microscope (T_a = 22 C). The needle of the assembly was inserted into the right interfemoral vein. Following insertion, the uropatagial membrane was stretched and a narrow strip of adhesive tape pressed firmly against the membrane to each side of the inserted needle to immobilize it and to prevent possible puncture of the blood vessels if animals moved. The operative procedure took less than 20 seconds and did not require occlusion of any major blood vessel.

Following the insertion of the cannula, leads between the implanted electrodes and the polygraph were connected. At a recorded heart rate of about 340 beats per minute, 1 μc of 86-Rb in 0.025 ml of saline was injected and the cannula flushed with 0.050 ml of heparinized saline.

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[5]Clay-Adams, 141 East 25 Street, New York, U.S.A.

After 120 heart beats, circulation was stopped within 1 to 3 seconds by injecting 0.10 ml saturated KCl via the cannula. The criterion for using the lapse of 120 heart beats as the interval between 86-Rb and KCl injections was based on preliminary studies (described below), which indicated that the amount of 86-Rb remaining per unit volume of blood changed least at this point and was approximately the same for non-hibernating and arousing bats.

The procedure for arousing bats was similar except that experiments were performed in the cold (T_a = 5 C), and the needle inserted during the first minute of arousal without the necessity of anaesthesia.

In preliminary studies, the isotope was injected into two groups of bats at heart rates 40 beats per minute (early arousal) and 480 beats per minute (late arousal). After 60, 120, 240, and 480 heart beats, saturated KCl was administered intravenously. Four to eight animals were sacrificed for each but the last experiment, for which only one bat was used. Radioactive rubidium was injected also into single individuals at heart rates 20, 60, 120, 240, 360, 480, and 800 beats per minute. These were sacrificed 60 seconds after the injection.

In subsequent arousal studies, the isotope was injected into groups of bats at heart rates 40, 80, 120, 180, 240, 300, 360, 480, 600, and 800 beats per minute in the winter, and at heart rates 40, 80, 120, 180, 240, 360, 480, 600, and 740 beats per minute (highest mean value) in the summer. Upon completion of arousal, two groups of bats (one in the winter and one in the summer) were transferred to the warm (T_a = 22 C). The isotope was injected 40 to 60 minutes later at a heart rate of 480 beats per minute. In these studies, 120 heart beats passed between 86-Rb and KCl injections.

For isotope injection of bats in deep hibernation, cannulae were pre-implanted. The method differed slightly for summer and winter experiments. During the summer, bats were allowed to hibernate for 5 to 8 days before cannulae were inserted as in arousing bats. After flushing the inserted cannula with heparinized saline, the tubing was closed off by turning the screw of the Tuohy-Borst adapter and the syringe removed. Most of the bats promptly re-entered deep hibernation when returned to their cages. The isotope was injected about 5 days later without removing bats from their cages.

The above method when used in winter studies evoked complete arousal. As an alternative, cannulae were implanted 5 to 10 hours after placing bats into the cold-room. After insertion of the cannula the tubing was flushed with heparinized saline, syringe and adapter removed, and the cannula sealed with a short, 30 gauge pin. All animals subjected to this method did enter hibernation in the winter. The isotope was injected two weeks later without removing bats from their cages, and by replacing the pin with a 30 gauge needle, attached to a syringe. To maintain these bats in deep hibernation, EKG electrodes were not attached. Low ventilation rates (1 breath every 2 to 3 minutes) were used as an indication of deep hibernation and 10 minutes (average HR in deep hibernation = 12 beats/minute) taken as the interval between 86-Rb and KCl injections. Of twelve experiments attempted, six were successful.

Following the injection of KCl, the thorax was opened, the heart excised, and blood allowed to drain into the chest cavity. This proved most effective in draining blood and preventing tissue contamination with

radioactive blood during dissection. The blood, collected with a hypodermic syringe, and the heart were placed in weighed scintillation counter vials. The chest cavity was cleansed thoroughly with moistened cotton swabs to remove traces of radioactive blood. These swabs together with about 2 ml of saline used for rinsing the hypodermic syringe were also placed in a scintillation counter vial.

Subsequent dissections were performed under a dissecting microscope. Drying of tissues was minimized by placing a humidifier next to the microscope and covering the entire apparatus with a plastic bag. Various tissues and organs were dissected free and placed into weighed counting vials. White fat, muscle, and carcass (remainder of body after removal of tissues examined), which comprise a relatively large mass, were put into small Erlenmeyer flasks. Anterior and posterior skeletal muscles were divided by cutting transversely across the rib cage below the diaphragm. The muscles were not separated from the bony skeleton. The bulk of mesenteric tissue was detached from the gastrointestinal organs. Vials and flasks, plus their contents, were reweighed and small amounts (2 to 3 ml) of nitric acid added. Tissues dissolved readily upon placing the glass containers into a water bath (70 to 80 C). Subsequently, the fluid level in vials was adjusted to the 4 ml gradation mark by addition of nitric acid. Similarly, the fluid level in flasks was adjusted to the 20 ml gradation mark, mixed thoroughly, and two 4 ml aliquots transferred from each flask to counting vials. A Nuclear Chicago well type scintillation counter (Model 1085) was used to assay organ radioactivity. Each sample was counted for ten minutes and the background radiation subtracted automatically. The readings obtained were corrected for

volume of aliquot counted, and the reading obtained for cotton swabs and saline was added to that for the blood. Organ radioactivities were expressed as a percentage of injected 86-Rb.

4. Estimation of organ blood flow. Cardiac output was not determined directly, but was approximated by substituting an estimated stroke volume and recorded heart rates in the formula:

Cardiac Output (CO) = Stroke Volume (SV) x Heart Rate (HR)

Since the estimated stroke volume of 3.0 ml per kilogram of body weight for the same species in flight (Studier and Howell, 1969) appeared too high, the blood volume a bat's ventricle can hold was approximated. This involved injecting methacrylate into hearts of six adult bats of an average size, comparable to that of the bats used in the blood distribution studies. The method utilized is described elsewhere (Rauch, 1968). The hardened plastic was removed from ventricles, and the amount of bat blood displaced by the cast was determined. An average of the six measurements, 0.024 ml, was taken as the estimated stroke volume. It should be mentioned that the hardening process of methacrylate, that is, the change from a methyl methacrylate monomer (liquid injected) to its polymer form (solid cast), involves shrinkage of about 10 percent. This brings the theoretical value for stroke volume somewhat closer to the actual value since the volume ejected during a ventricular contraction is always less than the volume of blood the ventricle can hold.

Assuming a constant stroke volume, cardiac output was calculated for different heart rates, and blood flow estimated according to the

formula:

$$\text{Organ blood flow rate (ml/min)} = \text{CO (ml/min)} \times \frac{\text{Organ activity (counts/min)}}{\text{Total injected activity (counts/min)} - \text{activity of blood (counts/min)}}$$

It should be re-emphasized that all values for capillary organ blood flow are based on the aforementioned assumptions and therefore represent theoretical values. Differences between approximated and true values must be expected. These, however, have little or no bearing on the primary interest of this study, which concerns relative changes in blood flow to various tissues and organs of *E. fuscus* during the arousal from hibernation.

4. Body Temperature Measurements

Body temperature, heart rate, and time were recorded simultaneously from 20 bats during arousal in winter. Teflon coated copper/constantan implant thermocouples[6] (wire size = 0.08 mm; insulated diameter 0.20 mm) were soldered to low resistance copper/constantan thermocouple wires and attached to a Speedomax W 12-channel potentiometer.[7] Three of the thermocouples were threaded through separate 27 gauge hypodermic needles (without a luer lock hub), and one pushed through a PE 20 polyethylene tubing. Hibernating bats were removed from their cages but left in the cold (T_a = 5 C). The thermocouple in the PE tubing was inserted about 1 cm into the colon and then taped to the uropatagium. The three thermocouples in needles were inserted superficially into the interscapular brown fat; anterior muscle at the lateral mid-thoracic region; and

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[6]Science Products Corp., 280 Route 46, Dover, New Jersey, U.S.A.

[7]Leeds and Northrop Co., 41 Constellation Court, Rexdale, Ontario, Canada.

posterior muscle, close to the trochanteric fossa. In some cases, it was possible to insert the colonic thermocouple further (3 to 4 cm) into the gut, thus measuring abdominal temperature.

D. STATISTICAL ANALYSIS

Statistical analysis of the data was performed by an IBM computer (University of Alberta Computer Center). The Student-Newman-Keuls procedure (Sokal and Rohlf, 1969) for unequal sample sizes was used to determine whether the differences between means are statistically significant. According to this procedure:

1. Sample means were arranged in the order of largest to smallest.
2. Means not significantly different from each other at the 5 percent (———) and 1 percent (- - -) level of probability were joined by lines.

As far as is known, the Student-Newman-Keuls procedure is the only procedure presently available for comparing more than two means from unequal sample sizes. For this reason it was used in the analysis of the data from this study, although the authors have not been able to comment on the degree of reliability of this relatively new statistical test.

RESULTS

HEART RATES

Heart rates for *E. fuscus* under different physiological conditions (Tables I and II) extend over a range from a low of 4 beats per minute in deep hibernation (T_a = 5 C) to a high of 800 beats per minute during peak arousal (T_a = 5 C). Because not all physiological states are considered, this study does not include maximum heart rates which are presumably obtained in flight and under experimental conditions of flight have been found to reach values as high as 1,200 beats per minute (Studier and Howell, 1969). Evidently, such wide ranges in heart rates have also been found in other species. *Myotis myotis*, which is only slightly larger (24 gm), when arousing under similar conditions has been found to attain a heart rate of approximately 700 beats per minute during peak arousal (Mejsnar and Jansky, 1970), and heart rates between 30 and 972 beats per minute have been reported for the much smaller (3.4 gm) small-headed bat, *Nannugo pipistrellus (Pipistrellus pipistrellus)*, by Buchanan (1911).

The extent to which heart rates of *E. fuscus* may vary under given conditions is delineated in Table I. Relatively wide ranges are evident for all but anaesthetized bats. Their heart rate values, on the other hand, are higher than those of sleeping bats. To interpret these findings, a number of factors must be considered. The ability of these mammals to lower their body temperature to near environmental temperatures during rest (heterothermy) presupposes corresponding reductions in heart

Table I. Heart rates of *E. fuscus* during different physiological conditions.

Number of animals	Physiological condition	Ambient temp. (C)	Heart rate (beats/min) Range
10	Non-hibernating resting	22	240-480
10	Non-hibernating sleeping	22	80-240
10	Non-hibernating anaesthetized	22	304-366
16	Hibernating	5	4- 16
105	Arousing from hibernation	5	20-800

Note: Number of animals (105) arousing from hibernation includes bats used for determining heart rates during arousal (page 13), bats used for body temperature measurements (page 22), and bats used for blood distribution studies during peak arousal and during post-arousal (pages 63 and 64, 69, 74).

rates since body temperature is possibly a major factor influencing heart rate. This by itself could explain the wide ranges in heart rates, at least during rest and sleep. If and to what extent direct neural control influences ranges in heart rates cannot be assessed from these findings but the ability of *E. fuscus* to alter heart rates almost instantaneously (Section: EKG) suggests involvement of some specific neural regulatory mechanism.

The higher heart rates of anaesthetized bats as compared to those of sleeping ones are taken as evidence that the animals were "lightly" anaesthetized (Section: Materials and Methods) and that, as in man, dog, rat, etc., Pentobarbital Sodium accelerates the heart of *E. fuscus* by its vagolytic effect (Nash *et al.*, 1956).

HEART RATE VERSUS TIME DURING AROUSAL

Heart rates were measured at intervals during arousal in the winter (Fig. 1) and in the summer (Fig. 2). Each point on the graph represents the mean value of 20 bats. Time zero (X-Y intercept) refers to the time when arousal stimulus (removing bats from cages) was applied. The lowest heart rates defined are those recorded 2 minutes after initial disturbance. Values for individual bats are presented in Appendix 1; mean values and standard deviations (s_d) in Table II and in Appendix 1. Heart rates and time during arousal of a single individual arousing during September, December, and February are depicted in Figure 3 and values presented in Table II.

All graphs, representing heart rate versus time during arousal, are sigmoid in shape. Heart rate increments are relatively small in early

Fig. 1. Heart rates (beats/minute) of *E. fuscus* as measured against time during arousal from hibernation (T_a = 5 C) in winter. Time zero (X-Y intercept) refers to the time when arousal stimulus (removing bat from cage) was applied. Each point on the graph represents the mean of 20 individuals.

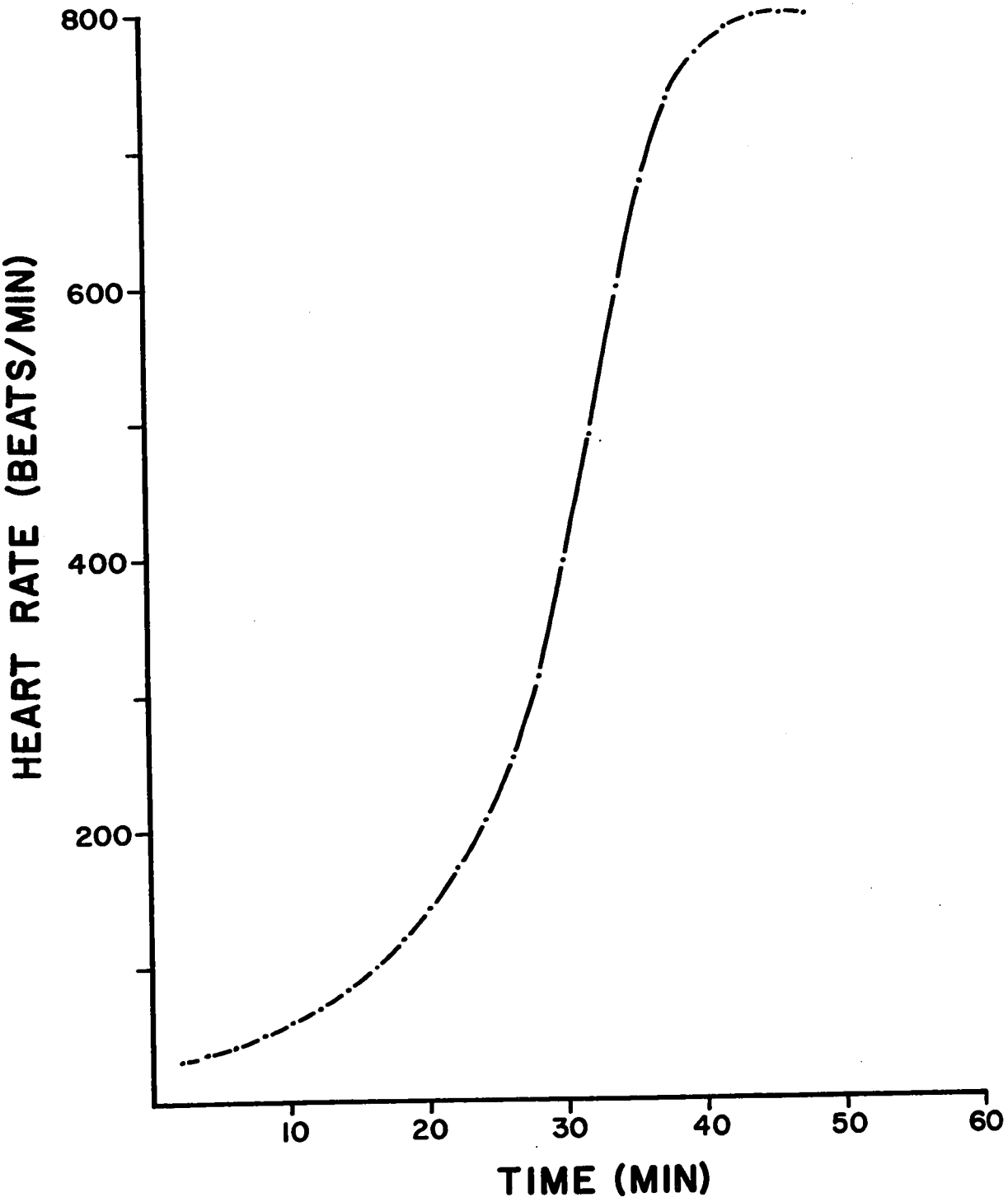

800
600
400
200
HEART RATE (BEATS/MIN)
10
20
30
40
50
60
TIME (MIN)

Fig. 2. Heart rates (beats/mimute) of *E. fuscus* as measured against time during arousal from hibernation (T_a = 5 C) in the summer. Time zero (X-Y intercept) refers to the time when arousal stimulus (removing bat from cage) was applied. Each point on the graph represents the mean of 20 individuals.

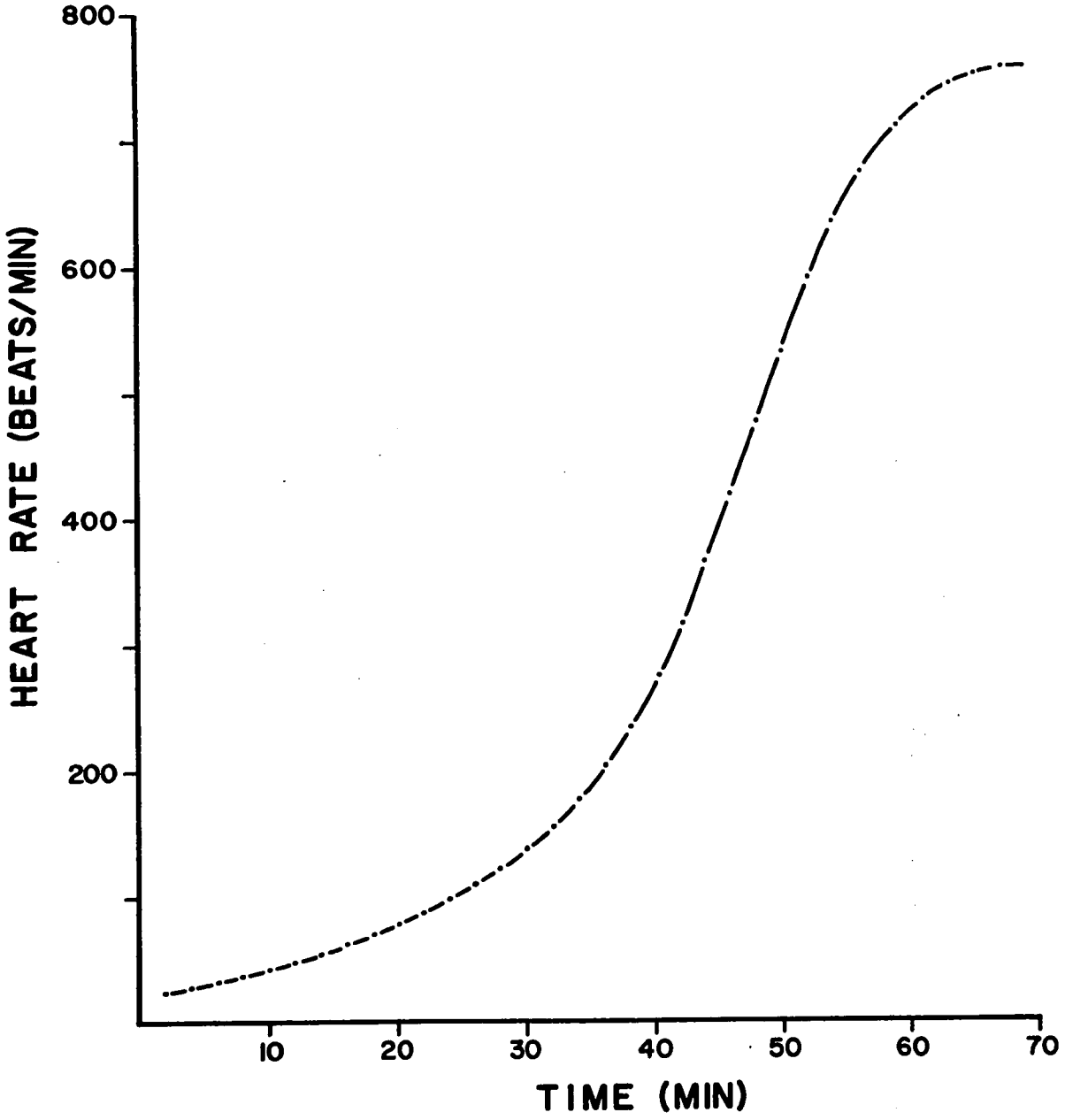

800
600
400
200
HEART RATE (BEATS/MIN)
10
20
30
40
50
60
70
TIME (MIN)

Fig. 3. Heart rates (beats/minute) of a single *E. fuscus* as measured against time during arousal from hibernation (T_a = 5 C) in September, December, and February. Time zero (X-Y intercept) refers to the time when arousal stimulus (removing bat from cage) was applied.

Table II. Heart rates (HR) in beats/minute of 2 groups of *E. fuscus* at 2-minute intervals during arousal from hibernation (T_a = 5 C) in the winter and in the summer, and of a single individual during December, February, and September. Values given for winter and summer studies represent the means and standard deviations (s_d) of 20 individuals each.

AROUSAL FROM HIBERNATION

Time (min) during arousal	Winter HR		Summer HR		December	February	September
	Mean	s_d (±)	Mean	s_d (±)	HR	HR	HR
2	30	2	24	4	32	32	30
4	36	2	29	4	36	34	34
6	41	3	34	4	42	40	38
8	49	3	38	4	52	44	40
10	58	5	44	6	62	50	44
12	70	5	49	7	76	58	48
14	82	7	56	8	90	64	52
16	98	7	62	9	108	76	58
18	118	10	70	8	130	88	62
20	141	12	78	9	156	98	68
22	171	13	86	10	188	110	72
24	205	23	96	12	228	128	80
26	252	29	108	11	360	148	84
28	312	42	121	13	480	170	92
30	398	62	136	14	648	198	100
32	490	72	155	15	724	228	110
34	599	70	177	18	764	168	120
36	676	57	204	23	784	308	130
38	737	38	236	29	796	368	144
40	770	26	275	40	800	440	156
42	790	14	316	48	800	570	172
44	799	5	363	53	800	694	190
46	799	4	419	68		742	210
48			476	81		780	234
50			532	86		784	268
52			589	81		796	310
54			635	72		800	390
56			676	58		800	520
58			711	55		800	640
60			732	42			696
62			747	36			720
64			749	30			734
66			752	25			740
68							748
70							748

arousal, but become extremely large during the late phase when the heart may accelerate by as much as 60 beats per minute per minute. The most obvious difference between winter and summer studies is the considerably shorter time required by bats to complete arousal in the winter. These animals also attain higher maximum heart rates during peak arousal.

Bats placed into the cold (T_a = 5 C) in summer do not arouse as readily as their winter counterparts. Of 30 animals, intended for heart rate studies, 10 individuals could not be aroused in the cold during early summer. Their heart rates accelerated slowly to approximately 120 beats per minute, then fluctuated between 120 and 180 beats per minute for 0.5 to 1.5 hours, when they were removed from the cold. Most of these bats recovered eventually and were able to arouse without difficulty during the following winter. That the ability to arouse in a cold environment depends largely on the season of the year is demonstrated also in Figure 3. The same individual aroused faster in February than in September, and fastest during December. Similar trends were seen in other bats during two successive years.

HEART RATE CHANGES AND EKG's

Electrocardiographic events are shown in Figures 4 through 18. Under various physiological conditions, *E. fuscus* can almost instantaneously double or triple a given heart rate and reduce it as rapidly by similar amounts (Figs. 6 to 18). Fourfold changes have been observed occasionally during entry into hibernation and during initial arousal. Abrupt reductions in heart rates, as revealed by lengthened R-R intervals (complete cycle of recorded cardiac events) of EKG's, occur during what

was presumed to be a transition from resting quiescently (Fig. 5) to falling asleep in non-hibernating bats (Fig. 6) and in bats after having completed arousal for approximately 1 hour (Fig. 15). Skipping of heart beats is most prevalent during entry into hibernation (Figs. 7 to 9) but occurs also during early arousal, typically between heart rates of 120 to 180 beats per minute in the summer (Fig. 13). Similar results were not obtained in bats arousing during the winter. Sudden heart rate increments, as a consequence of applied stimuli (touch or sound) occurred in deep hibernation and during sleep. In both conditions, the initial stimulus elicited a two- to fourfold increase in heart rate but further stimulation did not produce such drastic effects. Whereas stimulating bats in anaesthesia shows no detectable changes, skipping of heart beats occurs during recovery from anaesthesia (Fig. 18).

Electrocardiograms of *E. fuscus* show a number of characteristics similar to those of other hibernators (Johansson, 1969). Distinct P, QRS, and T waves (Fig. 4), representing atrial depolarization, ventricular depolarization, and ventricular repolarization, respectively, are present. As in most hibernators which have been investigated, the S-T segment is absent in big brown bats. There is no indication of a J wave (positive deflection between QRS complex and T wave), a typical finding of unknown nature in the hypothermic rat, dog, and man (Johansson, 1969). As in other hibernators, there are differences in magnitude and duration of EKG's between hibernating and non-hibernating bats. Although these changes can be explained largely in terms of direct temperature effects on the myocardium, ionic shifts and enzymatic modifications are probably also involved (Johansson, 1969).

Fig. 4. EKG of *E. fuscus* in deep hibernation (T_a = 5 C) as obtained from bipolar recording. The various components, representing cardiac events, are illustrated.

R-R interval: complete cycle of cardiac events

P wave : atrial depolarization

QRS complex : ventricular depolarization

T wave : ventricular repolarization

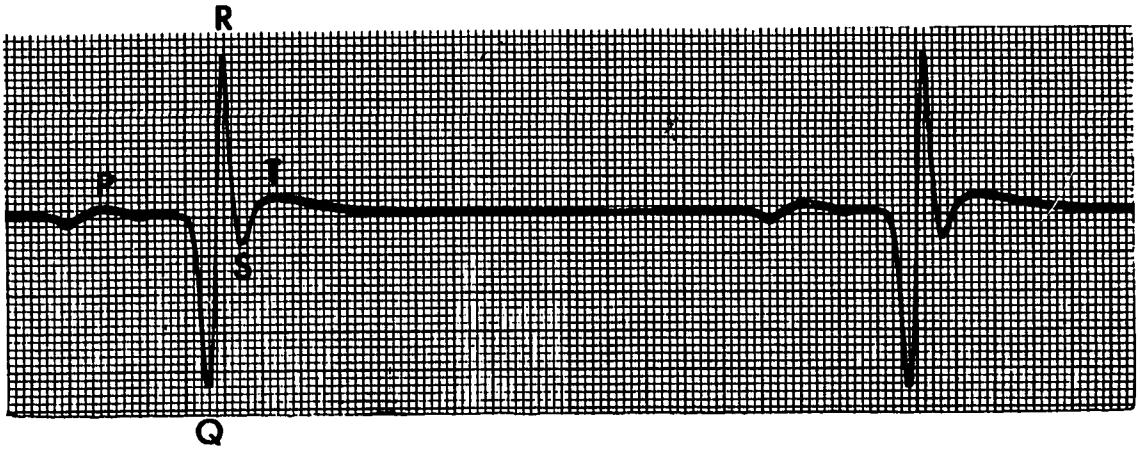
(paper speed = 10 mm/sec)

Fig. 5. EKG of non-hibernating *E. fuscus*, resting quiescently at room temperature (T_a = 22 C).

(paper speed = 50 mm/sec)

Fig. 6. EKG of non-hibernating *E. fuscus*, presumably in a transition from resting quiescently to falling asleep (T_a = 22 C). There is a sudden change in heart rate from about 300 beats/min to about 160 beats/min.

(paper speed = 50 mm/sec)


R
P
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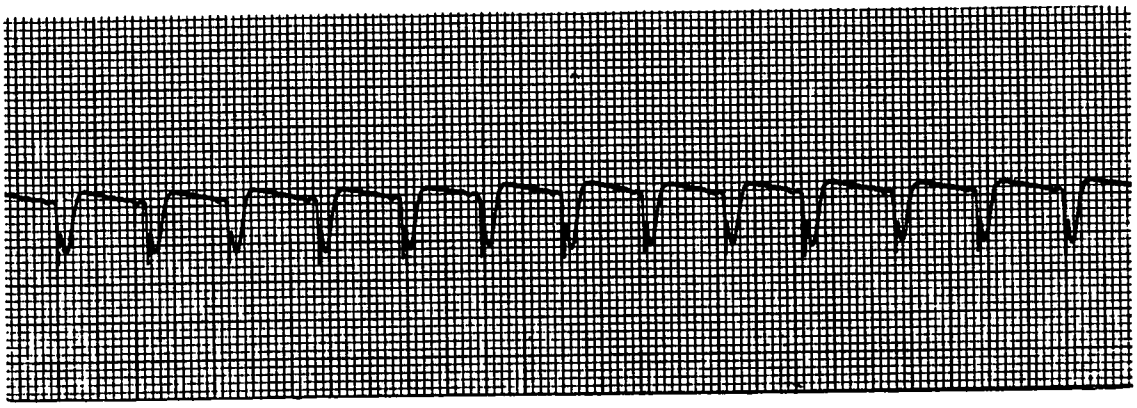

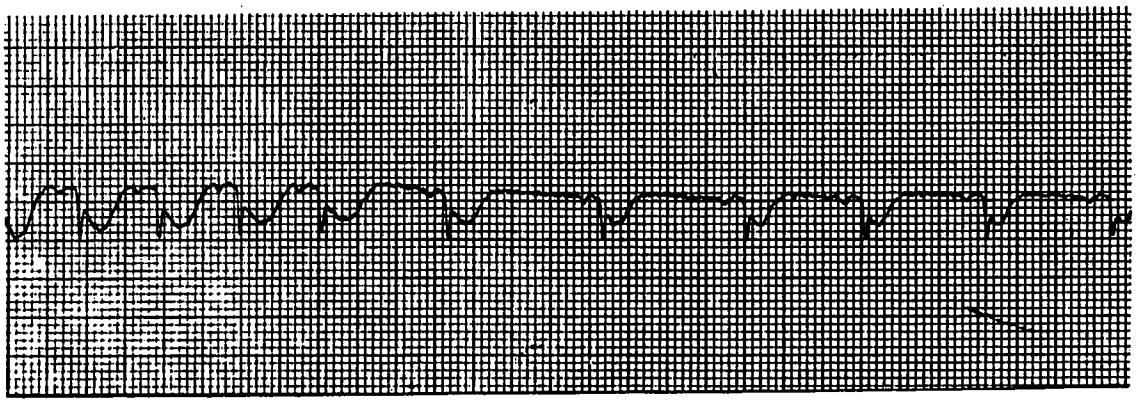

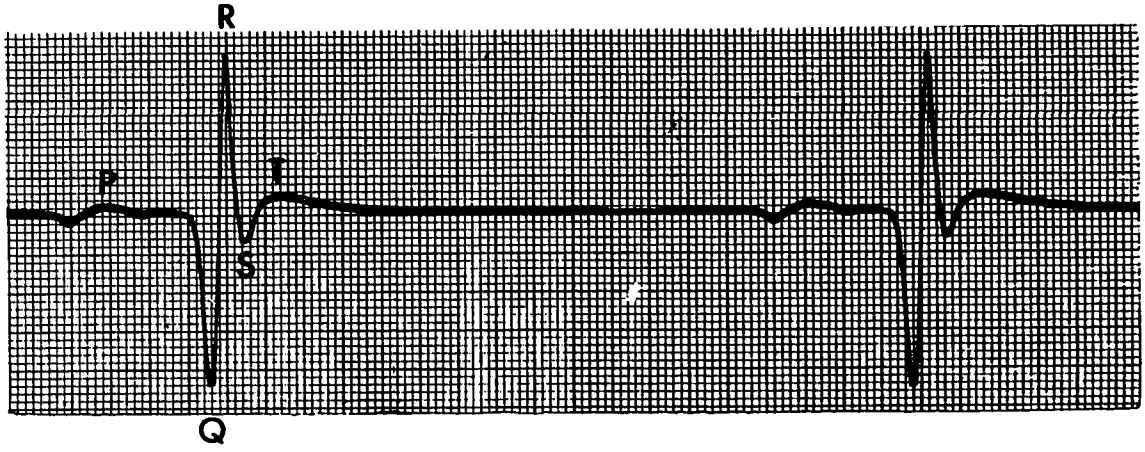
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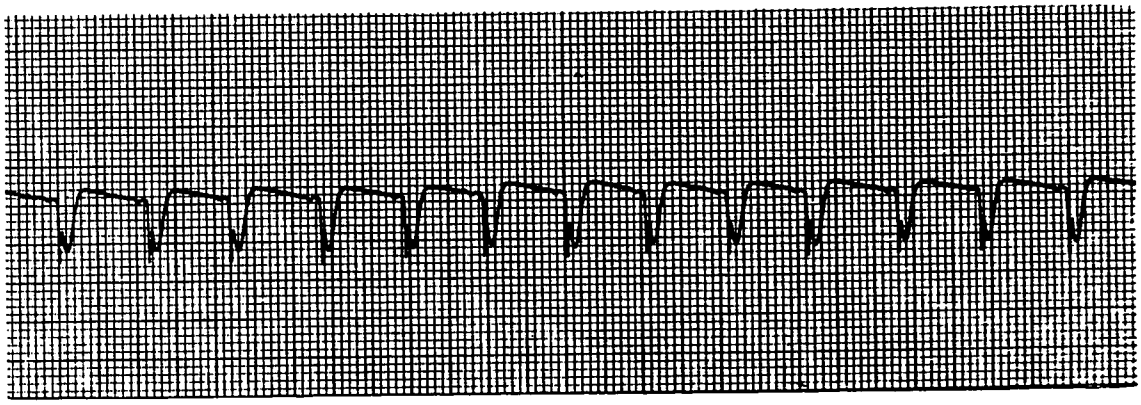


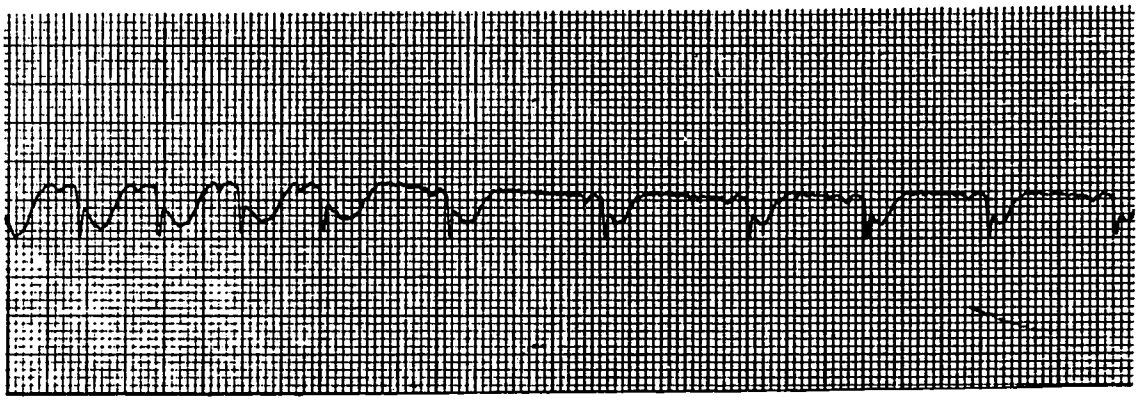


Fig. 7. EKG of *E. fuscus* during entry into hibernation. The record was obtained after the animal had been in the cold (T_a = 5 C) for 24 hours. Skipping of heart beats is very prominent and occurs at irregular intervals.

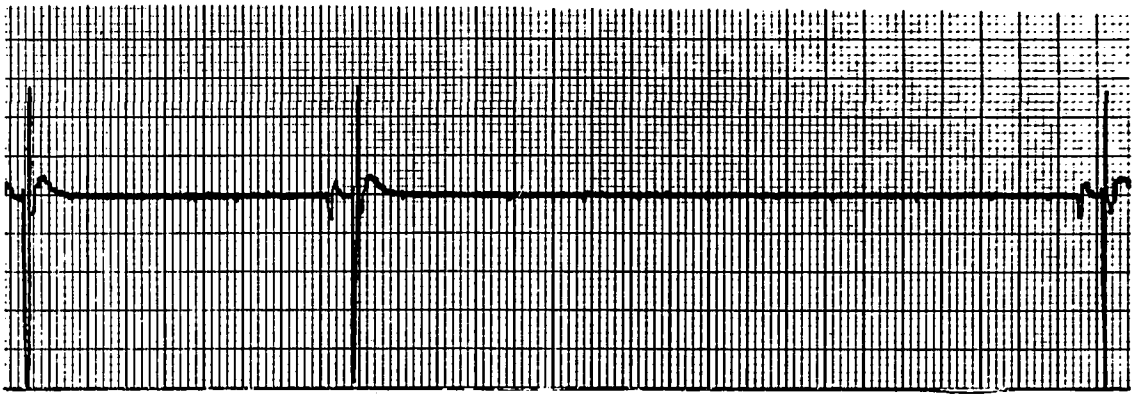
(paper speed = 5 mm/sec)

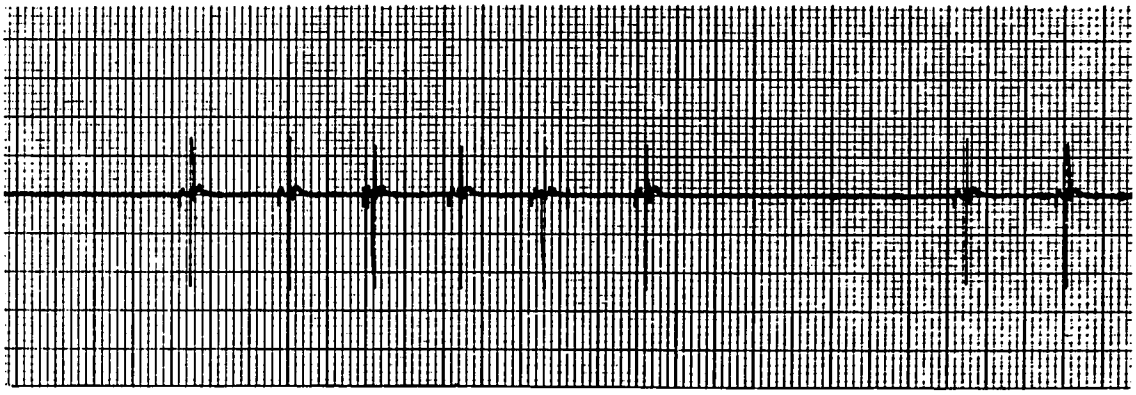
Fig. 8. EKG of *E. fuscus* during entry into hibernation. The record was obtained after the animal had been in the cold (T_a = 5 C) for 24 hours. Skipping of heart beats is very prominent and occurs at irregular intervals. EKG's depicted in Figures 7 and 8 are from the same individual.

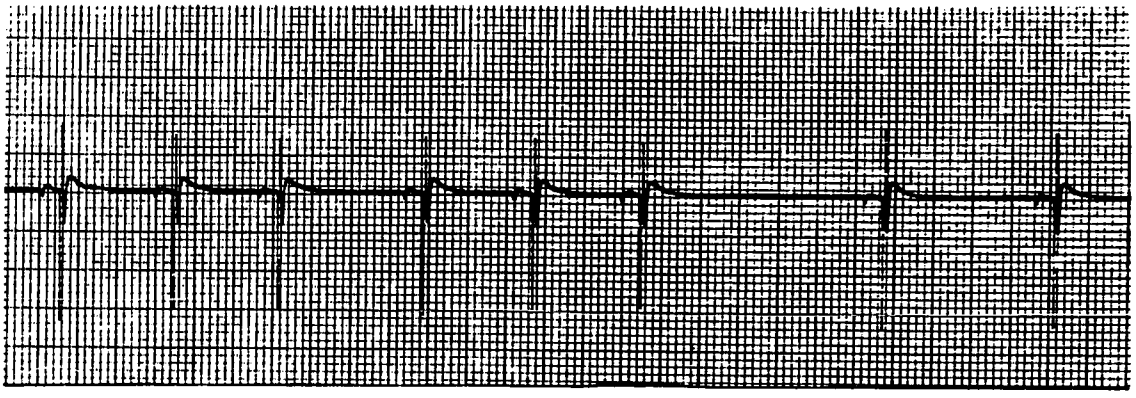
(paper speed = 2.5 mm/sec)

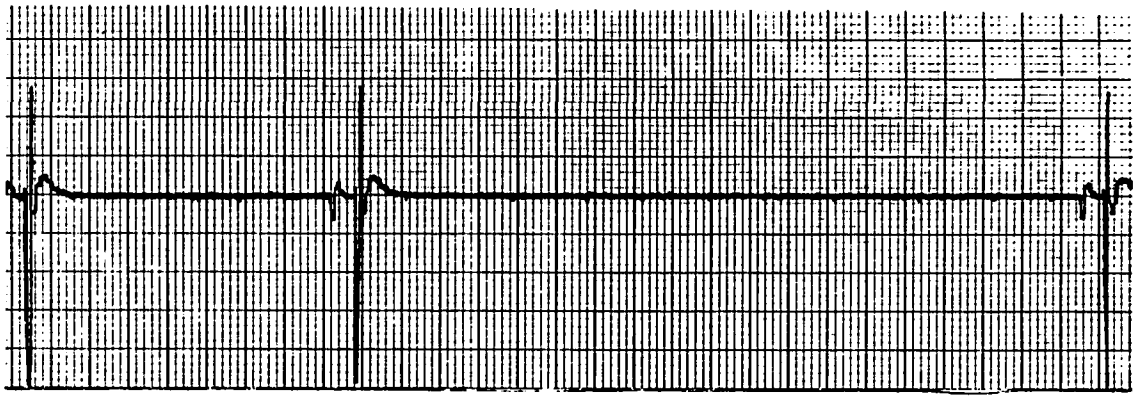
Fig. 9. EKG of *E. fuscus* during entry into/or in early hibernation. The record was obtained after the animal had been in the cold (T_a = 5 C) for 48 hours. Skipping of heart beats is very prominent and occurs at irregular intervals.

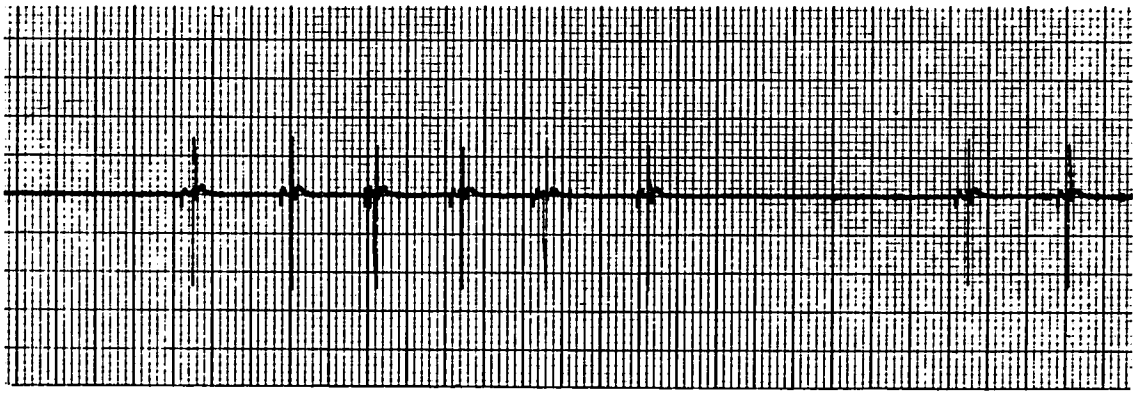
(paper speed = 2.5 mm/sec)











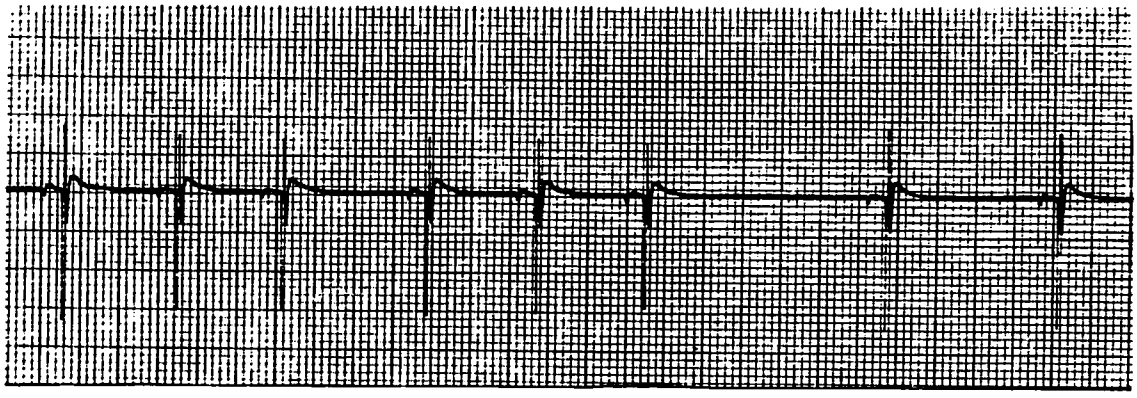


Fig. 10. EKG of *E. fuscus* in deep hibernation. The record was obtained after the animal had been in the cold (T_a = 5 C) for 1 week. Heart beats are regular.

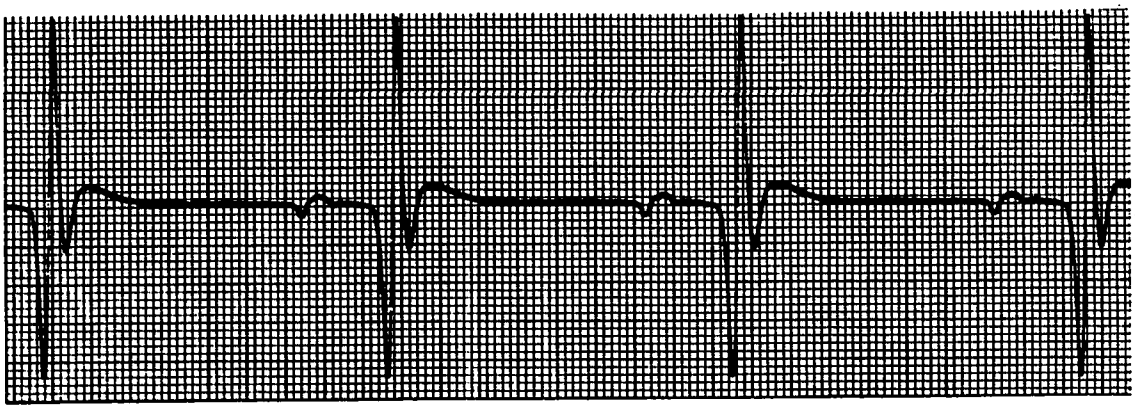
(paper speed = 5 mm/sec)

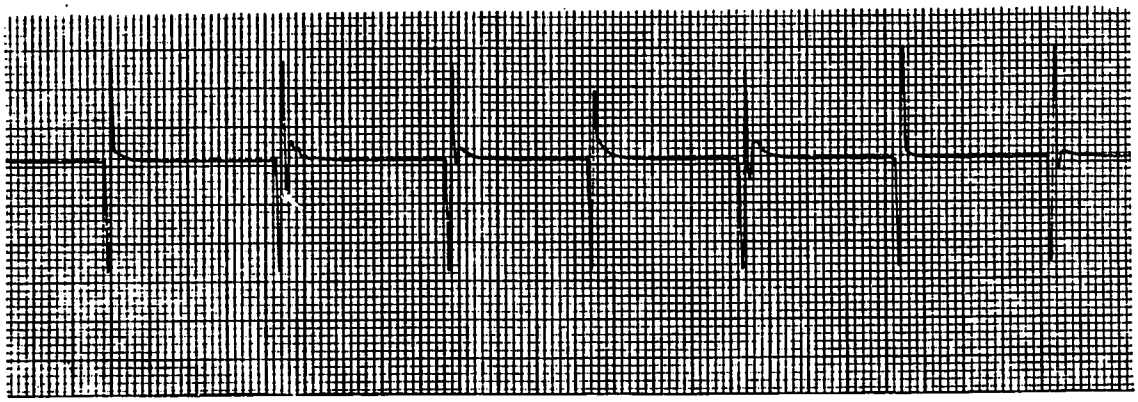
Fig. 11. EKG of *E. fuscus* prior to death. The record was obtained after the animal had been in the cold (T_a = 5 C) for 10 days during the summer. The P wave is absent; T wave starts to disappear.

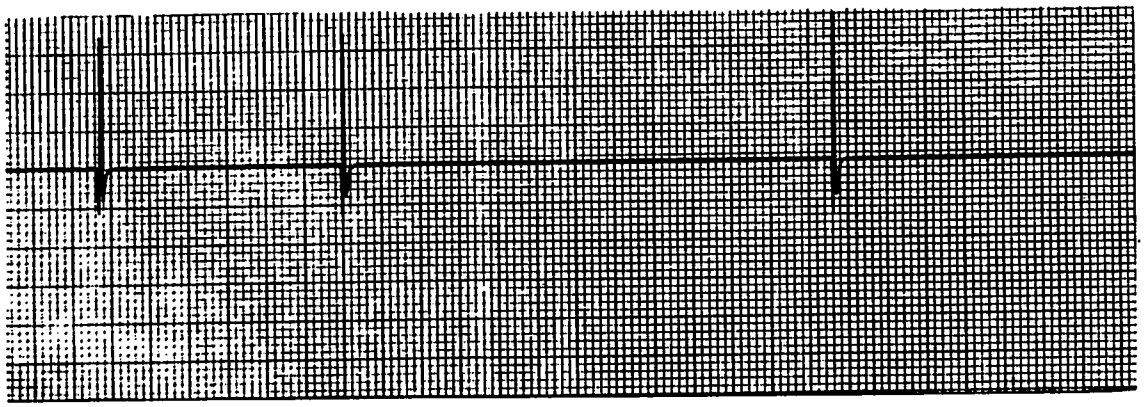
(paper speed = 5 mm/sec)

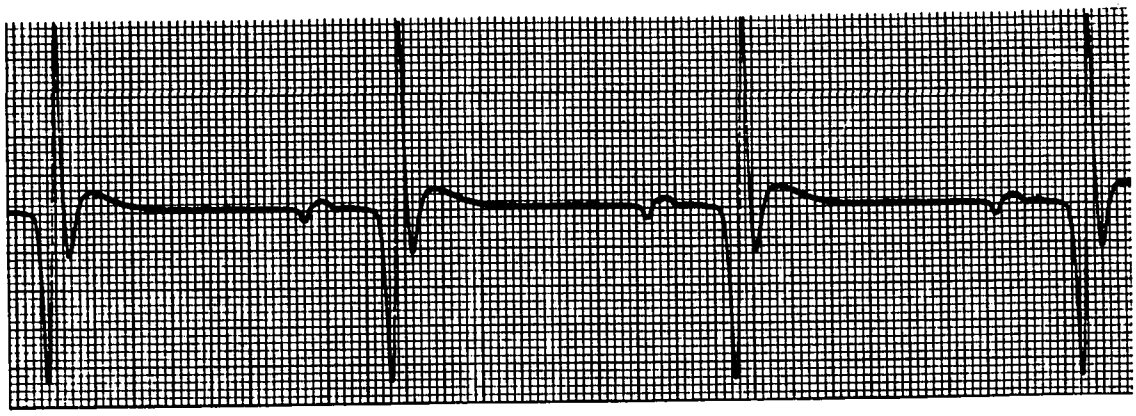
Fig. 12. EKG of *E. fuscus* during death. The record was obtained after the animal had been in the cold (T_a = 5 C) for 10 days during the summer. The P and T waves are absent. EKG's depicted in Figures 11 and 12 are from the same individual.

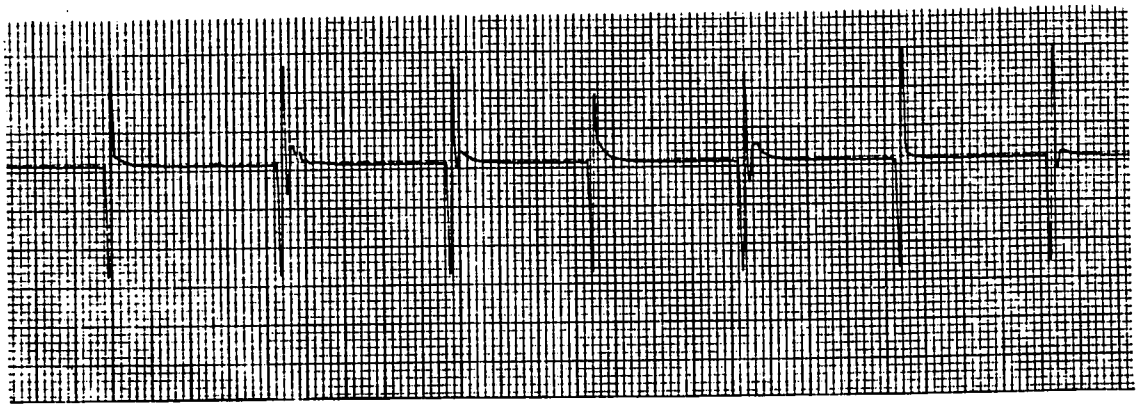
(paper speed = 1 mm/sec)











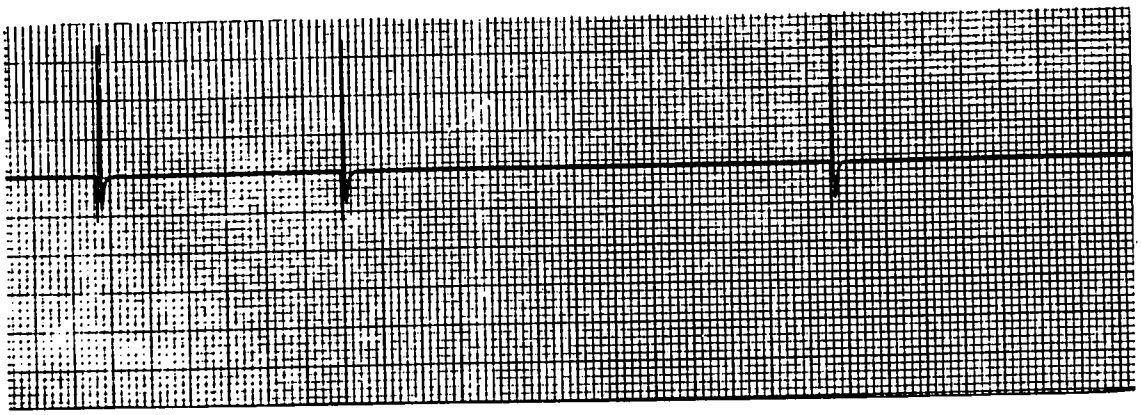


Fig. 13. EKG of *E. fuscus* during arousal from hibernation (T_a = 5 C) in the summer. Skipping of heart beats set in as the animal reached a heart rate of about 120 beats/min.

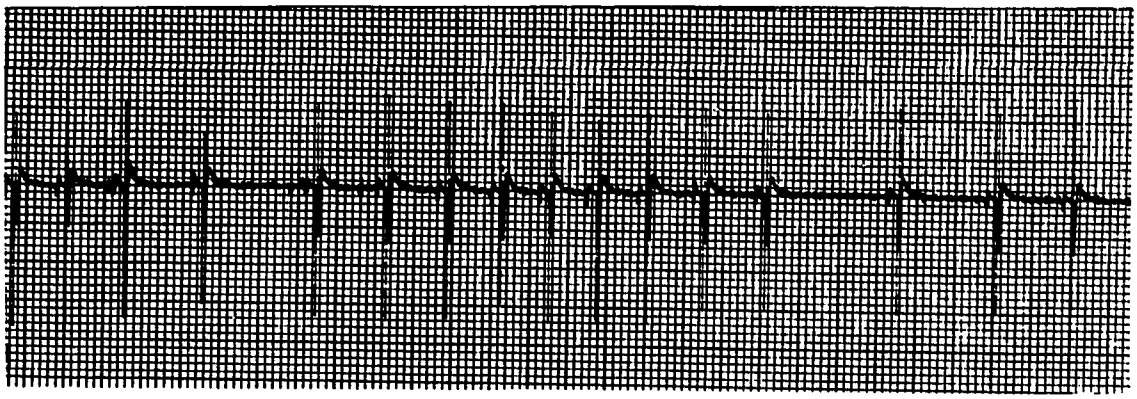
(paper speed = 25 mm/sec)

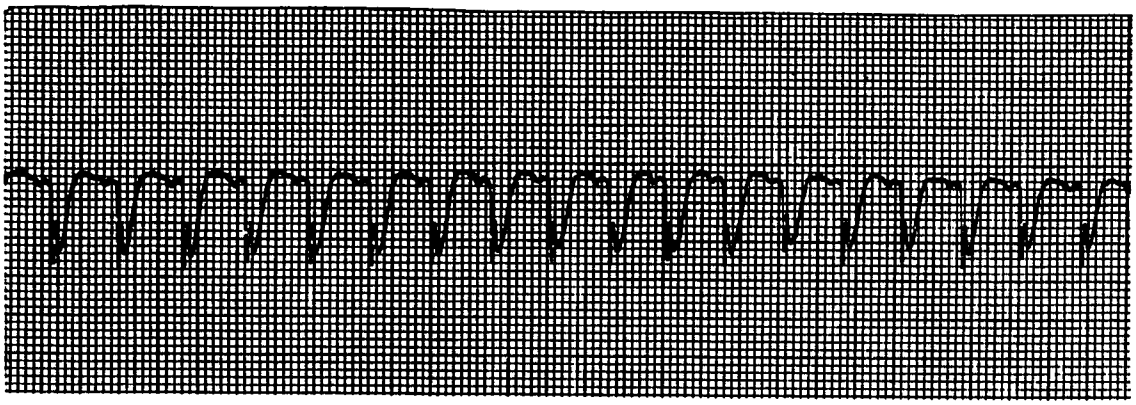
Fig. 14. EKG of *E. fuscus* during peak arousal from hibernation (T_a = 5 C) in the winter. Heart beats are regular.

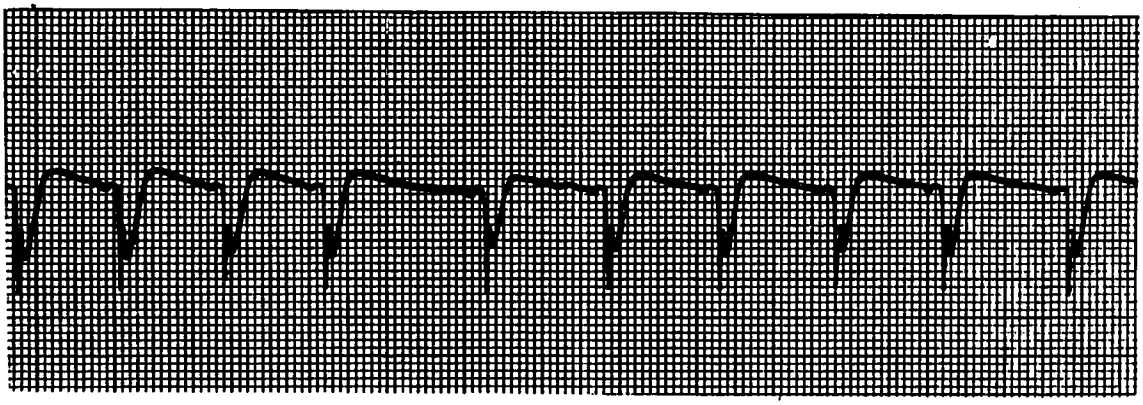
(paper speed = 100 mm/sec)

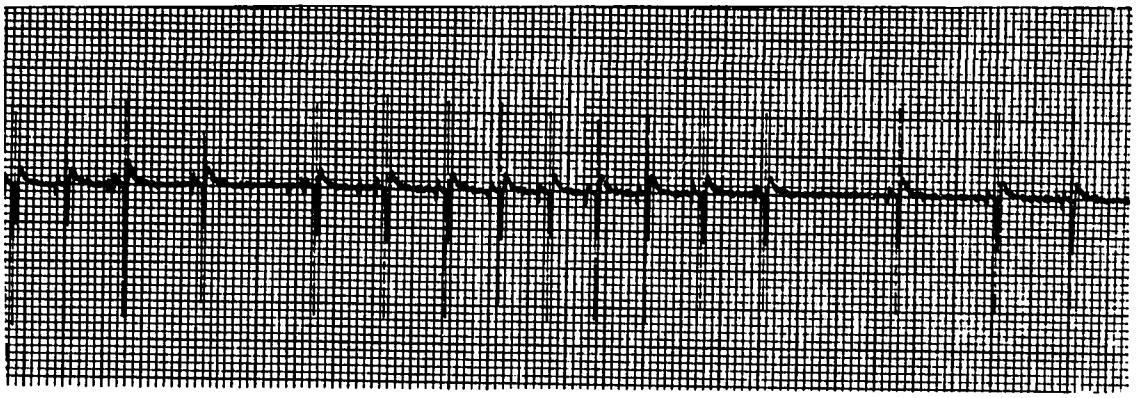
Fig. 15. EKG of *E. fuscus* having completed arousal from hibernation (T_a = 5 C) in the winter. The record was obtained after the animal had been in the warm (T_a = 22 C) for 1 hour and was resting quiescently. Heart beats are irregular. Occasional skipping of heart beats can be observed.

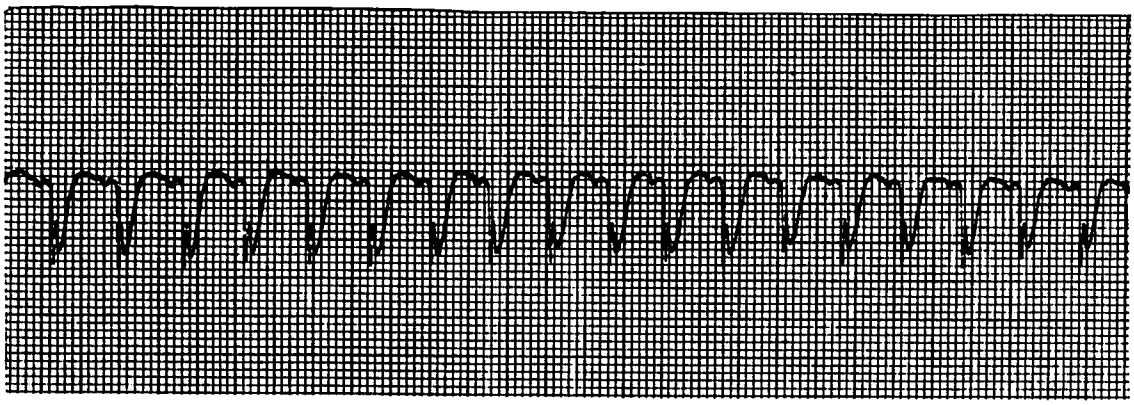
(paper speed = 100 mm/sec)











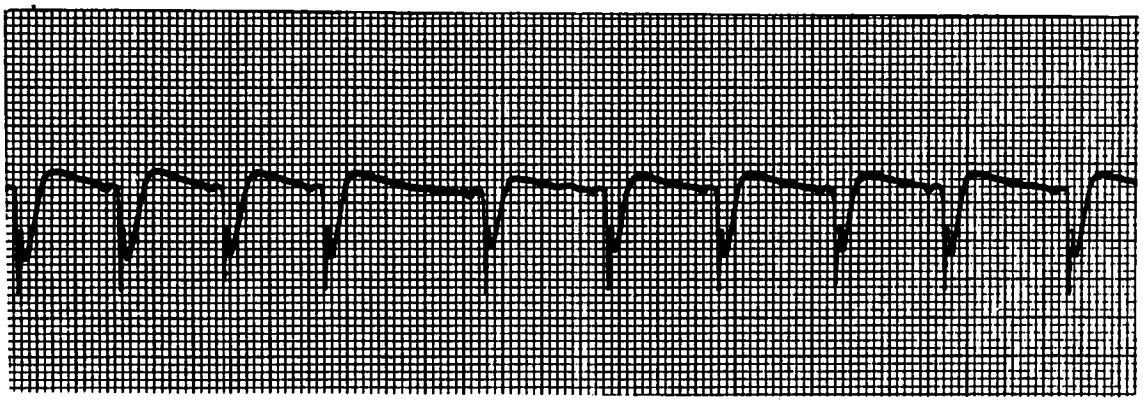


Fig. 16. EKG of *E. fuscus*, unable to arouse from hibernation in the cold (T_a = 5 C) during the summer. Consequently, the animal was transferred to the warm (T_a = 22 C) and the record obtained 2 hours later. The EKG shows an apparent prolongation between QRS complex and T wave.

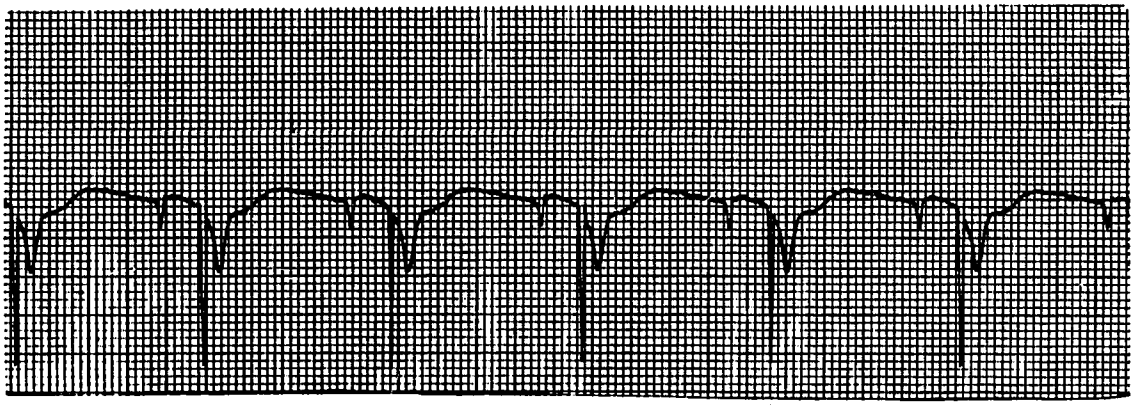
(paper speed = 50 mm/sec)

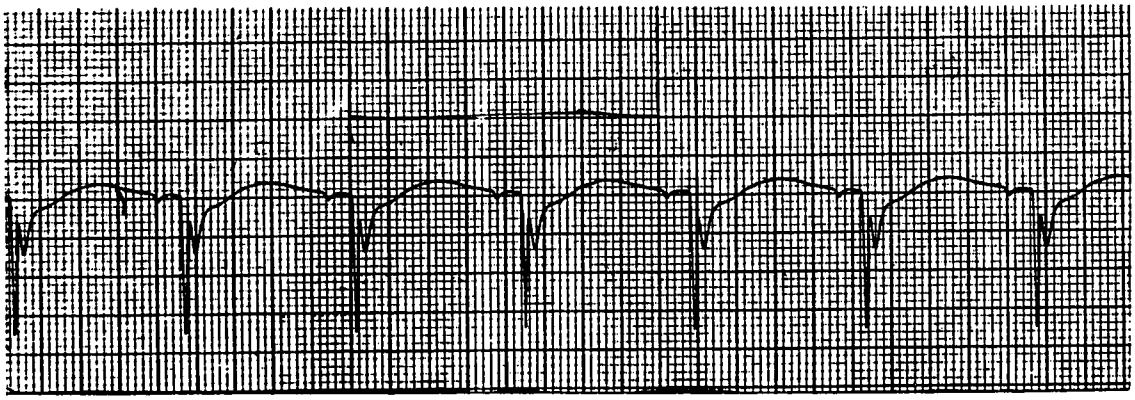
Fig. 17. EKG of *E. fuscus* deeply anaesthetized with Pentobarbital Sodium (80 mg/kg body weight). The animal was kept at room temperature (T_a = 22 C). The EKG shows an apparent prolongation between QRS complex and T wave.

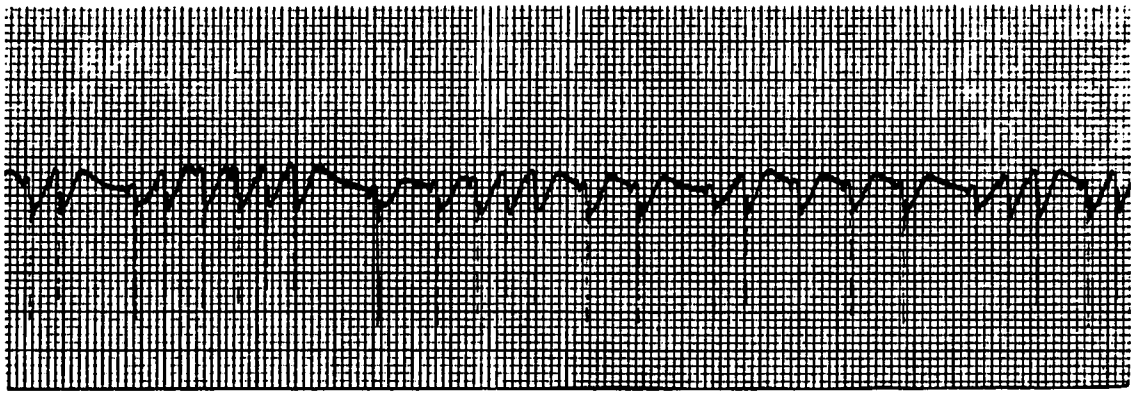
(paper speed = 50 mm/sec)

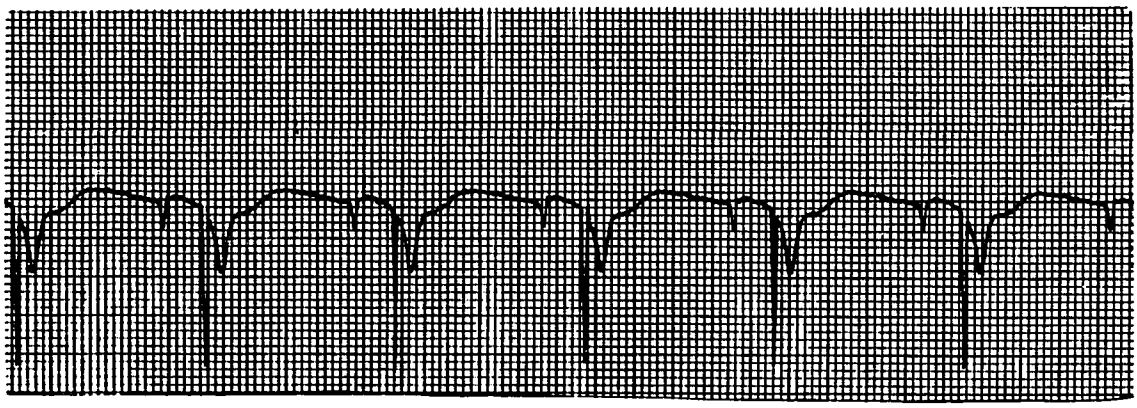
Fig. 18. EKG of *E. fuscus* during recovery from anaesthesia (T_a = 22 C). Irregular heart beats and skipping of heart beats can be observed.

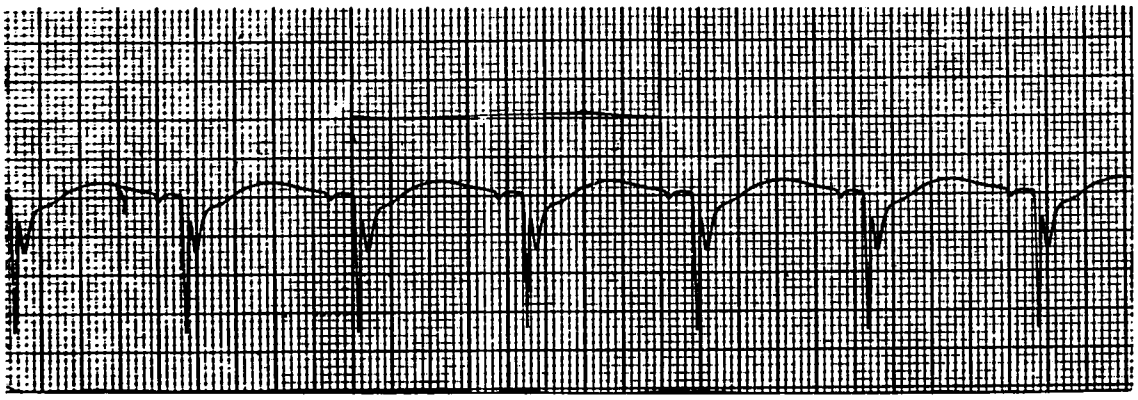
(paper speed = 50 mm/sec)

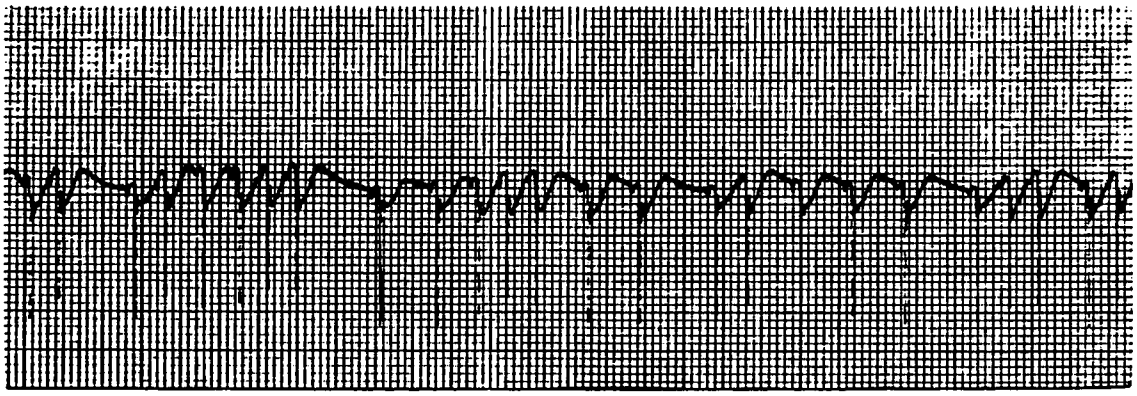












Although this study did not concern details of cardiac events, some noteworthy features can be seen in EKG recordings. These appear to be a prolongation between the QRS complex and the T wave in EKG's of anaesthetized bats (Fig. 17) and of those considered to be incapable of arousing in the cold during the summer (Fig. 16). This has not previously been demonstrated. Like other individuals that were unable to arouse, the bat whose EKG is presented in Fig. 16, showed fairly regular heart rate increments in early arousal until a heart rate of about 120 beats per minute was reached. Subsequently, skipping of heart beats occurred and heart rates fluctuated between 120 and 180 beats per minute for a period of about 1 hour when the animal was removed from the cold. Although heart beats became regular within 1 hour in the warm (T_a = 22 C), the heart rate did not increase significantly until 4 hours later when values of 500 beats per minute were obtained and S-T prolongation disappeared. The striking similarity of these EKG's (Figs. 16 and 17) is conspicuous and leads to a number of questions. Are the factors influencing ventricular repolarization in anaesthetized bats and presumably hypothermic bats the same? Is there a correlation between depressed vagal function and a prolonged S-T interval? Acetylcholine is known to enhance ventricular repolarization in frogs but such effects have not been demonstrated in cats and dogs (Hoffman and Cranefield, 1960). On the other hand, since there are morphological (Nielson and Owman, 1968) and functional differences (Johansson, 1969) between the hearts of mammalian hibernators and non-hibernators, no deductions can be made from these findings.

ORGAN, TISSUE, AND BODY WEIGHTS

Absolute organ, tissue, and body weights of 94 bats studied in the winter and 59 bats (49 hibernating and 10 non-hibernating) studied in the summer are presented in detail in Appendix 2 (Tables 1, 4, and 7). Mean values and results from statistical analysis are summarized in Tables III and IV. Organ and tissue weights, expressed as percentages of semi-lean and lean body weights, are given in detail in Appendix 2 (Tables 2, 5, 8, and 3, 6, 9, respectively). Mean percentage weights of various tissues and organs, and results from statistical analysis are shown in Tables V and VI. Semi-lean body weight refers to the total body weight minus the weight of white adipose tissue (W.A.T.), and lean body weight refers to the total body weight minus the weights of both white and brown adipose tissue. To express organ and tissue weights (other than those of brown and white adipose tissue) as percentages of lean weight rather than as percentages of total body weight minimizes errors due to seasonal differences in body fats. The percentages of brown and white adipose tissues can be expressed accurately only as percentages of semi-lean and total body weights, respectively.

Absolute weights of most organs from bats arousing in the winter are higher than those from bats arousing in summer (Table IV). Not significantly different are their kidney, stomach, intestinal and total muscle weights. Most organ weights from non-hibernating bats fall in between those of the two groups, but they do have the highest total muscle and stomach weights, and the lowest kidney and intestinal weights. Considering that the mean lean body weight of bats studied in winter is about 5 percent higher than that of non-hibernating bats, it is

Table III. Mean organ, tissue and body weights (wt.) in grams (gm) of *E. fuscus*, sacrificed during experimentation in winter and summer.

Organ or tissue	GROUP A SUMMER EXPT. Non-hibernating anaesthetized (T_a = 5 C) N = 10		GROUP B WINTER EXPT. Arousal from hibernation (T_a = 5 C) N = 94		GROUP C SUMMER EXPT. Arousal from hibernation (T_a = 5 C) N = 49	
	Mean wt. (gm)	s_d (±)	Mean wt. (gm)	s_d (±)	Mean wt. (gm)	s_d (±)
Skin	1.9916	0.0785	1.9959	0.3595	1.7004	0.3092
Muscle ant. body	4.1298	0.5736	3.9645	0.4910	3.6982	0.5168
Muscle post. body	1.3346	0.1814	1.4717	0.1739	1.3145	0.1697
Total muscle	5.4644	0.7371	5.4362	0.6309	5.0127	0.6638
Diaphragm	0.1000	0.0140	0.1133	0.0159	0.0960	0.0223
Interscap. B.A.T.	0.2907	0.1575	0.4834	0.0993	0.2279	0.1191
Other B.A.T.	0.2709	0.1000	0.4507	0.0944	0.2263	0.1154
Total B.A.T.	0.5344	0.2286	0.9338	0.1820	0.4542	0.2298
Liver	0.7022	0.0840	0.7534	0.1621	0.6505	0.1028
Kidneys	0.1542	0.0204	0.1852	0.0383	0.1804	0.0309
Stomach	0.1816	0.0210	0.1396	0.0287	0.1411	0.0270
Intestine	0.3398	0.0745	0.5783	0.1284	0.5432	0.1209
Myocardium	0.1289	0.0169	0.1482	0.0213	0.1280	0.0149
Blood	1.0878	0.0686	1.4316	0.1724	1.1570	0.1354
W.A.T.	1.5089	1.2190	5.1042	2.2986	1.0621	0.9487
Carcass	5.4270	0.3807	5.4987	0.6051	5.0145	0.4441
Total body wt.	17.6388	1.5988	22.3188	3.2628	16.1401	1.9435
Semilean body wt.	16.1300	1.1745	17.2146	2.9252	15.0780	1.4281
Lean body wt.	15.5956	1.2285	16.2808	1.7012	14.6239	1.4135

Table IV. Results from statistical analysis (Student-Newman-Keuls procedure) on absolute organ, tissue, and body weights of *E. fuscus*.

Skin:	W N S	Muscle ant. body:	N W S	Muscle post. body:	W N S	Total muscle:	N W S
Diaphragm:	W N S	Interscap. B.A.T.:	W N S	Other B.A.T.:	W N S	Total B.A.T.:	W N S
Liver:	W N S	Kidneys:	W S N	Stomach:	N S W	Intestine:	W S N
Myocardium:	W N S	Blood:	W S N	W.A.T.:	W N S	Carcass:	W N S
Total body wt.:	W N S	Semilean body wt.:	W N S	Lean body wt.:	W N S		

N: refers to mean weight of organ or tissue of non-hibernating bats, sacrificed during the summer.

W: refers to mean weight of organ or tissue of bats, sacrificed during arousal from hibernation in the winter.

S: refers to mean weight of organ or tissue of bats, sacrificed during arousal from hibernation in the summer.

Table V. Mean organ and tissue weights (wt.), expressed as a percentage of lean body weights, of *E. fuscus*, sacrificed during experimentation in winter and summer.

Organ or tissue	GROUP A SUMMER EXPT. Non-hibernating anaesthetized (T_a = 22 C) N = 10		GROUP B WINTER EXPT. Arousal from hibernation (T_a = 5 C) N = 94		GROUP C SUMMER EXPT. Arousal from hibernation (T_a = 5 C) N = 49	
	Percentage mean wt.	s_d (±)	Percentage mean wt.	s_d (±)	Percentage mean wt.	s_d (±)
Skin	12.81	1.95	12.23	1.48	11.59	1.54
Muscle ant. body	26.32	1.94	24.36	1.76	25.23	1.81
Muscle post. body	8.54	0.80	9.04	0.54	8.97	0.54
Total muscle	34.86	2.57	33.40	1.86	34.20	2.04
Diaphragm	0.64	0.07	0.70	0.07	0.66	0.15
Liver	4.51	0.52	4.61	0.75	4.45	0.60
Kidneys	0.99	0.11	1.13	0.18	1.24	0.17
Stomach	1.17	0.18	0.86	0.14	0.96	0.16
Intestine	2.17	0.39	3.55	0.68	3.74	0.83
Myocardium	0.82	0.08	0.91	0.11	0.88	0.09
Blood	6.99	0.45	8.82	0.87	7.93	0.78
Carcass	34.74	1.51	33.79	1.79	34.34	1.41
	Percentage of semilean body weight					
Total B.A.T.	3.52	1.61	5.46	1.10	3.01	1.50
	Percentage of total body weight					
W.A.T.	8.24	5.94	22.12	7.17	6.19	5.06

Table VI. Results from statistical analysis (Student-Newman-Keuls procedure) on percentage organ and tissue weights of *E. fuscus*.

Skin:	N	Muscle ant. body:	N	Muscle post. body:	W	Total muscle:	N				
	W		S		S		S				
	S		W		N		W				
Diaphragm:	W	Liver:	W	Kidneys:	S	Stomach:	N				
	S		N		W		S				
	N		S		N		W				
Intestine:	S	Myocardium:	W	Blood:	W	Carcass:	N				
	W		S		S		S				
	N		N		N		W				
Total B.A.T.:	W	W.A.T.:	W								
	N		N								
	S		S								

N: refers to mean weight of organ or tissue of non-hibernating bats, sacrificed during the summer.

W: refers to mean weight of organ or tissue of bats sacrificed during arousal from hibernation in the winter.

S: refers to mean weight of organ or tissue of bats sacrificed during arousal from hibernation in the summer.

conspicuous to note that the kidney and intestinal weights are about 20 percent higher and stomach weight 20 percent lower in the winter bats. It might reflect weight changes in these organs during hibernation or in preparation for it. Absolute increments in lung, heart, and kidney weights have been reported for hibernating golden hamsters (Smit-Vis and Smit, 1969). Although possible weight changes of digestive organs have not been investigated, present observations suggest that greater amounts of mucous in the lining of the gut could account for the higher intestinal weight in bats studied during the arousal process.

On a percentage weight basis, there is no significant difference in skin, diaphragm, liver, and carcass from the three groups of bats. Their percentage lean weights of total muscle, lowest in bats studied during arousal in winter, is significantly different at the 5 percent level but not at the 1 percent level of probability. Percentage weights of stomach and intestine are similar in the two groups of arousing bats but the former is significantly higher and the latter significantly lower in non-hibernating bats. Percentage weights of kidneys, white adipose tissue, and collected blood are significantly different at the 5 percent and 1 percent level of probability in all groups. Brown adipose tissue, not grossly different in the two groups studied during the summer, is considerably higher in bats studied during the winter. Considerable increments in the masses of brown adipose tissue in late autumn have been observed previously in little brown bats (Rauch, 1968) and this study confirms similar changes for big brown bats. A twofold increase in the thickness of the basement membrane of renal glomeruli, which has been demonstrated in hibernating thirteen-lined ground squirrels (Zimny and

Rigamer, 1966) and in hibernating little brown bats, *Myotis lucifugus* (Rosenbaum *et al.*, 1967), might be expected to result in a weight increase of this organ during hibernation. Whether a similar occurrence accounts for or contributes to the differences in the weights of kidneys between hibernating and non-hibernating *E. fuscus* is open to speculation at this time. Blood volume increments in deep hibernation have been reported for a few hibernators (Kayser, 1961). Working with golden hamsters, Lyman *et al.* (1957) attributed the increase in the ratio: blood volume x 100/body weight, to a decrease in body weight. Present data suggest, but do not prove, that blood volume might increase in hibernating bats.

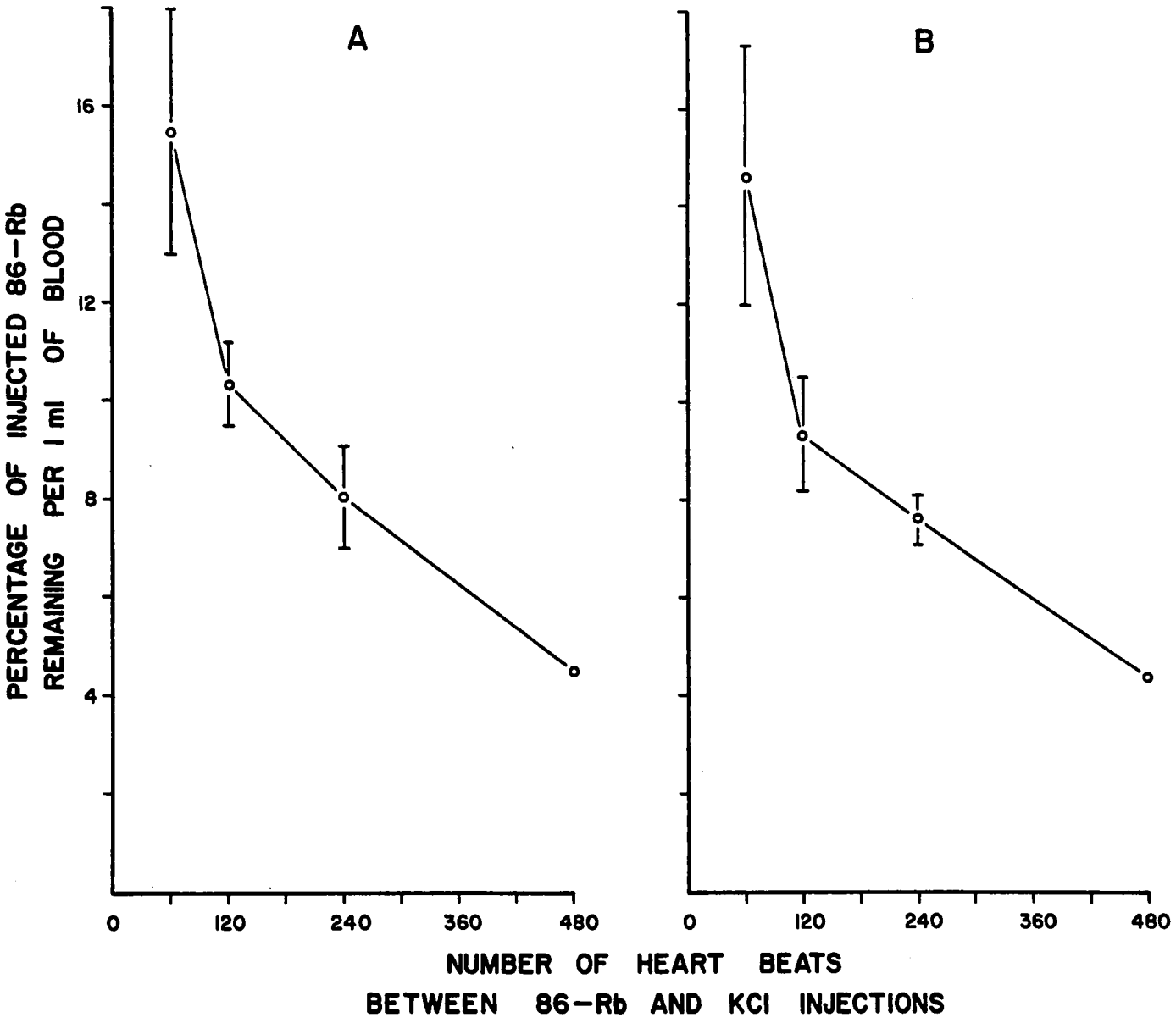
PRELIMINARY 86-Rb STUDY

The percentage of injected isotope remaining in the blood at a given interval following intravenous 86-Rb injection was used as an index in determining if low body temperatures have a gross effect on the uptake of rubidium by tissues of the experimental animal. The reliability of this index necessitates the following explanation. Studies performed in normothermic, non-hibernating mammals indicate that all organs except the brain have similar extraction ratios for the isotope between 9 and 64 seconds following its intravenous injection. Therefore, during this time the percentage of 86-Rb taken up by organs (except the brain) equals the fraction of cardiac output delivered to them (Sapirstein, 1958). Other evidence indicates that radioactive rubidium is a flow-limited substance, extracted effectively across capillary beds but not across arterio-venous shunts (Friedman, 1968; 1971; Mayerle and Havel, 1969) and its back-

diffusion is minimal (Friedman, 1969). Uptake of the isotope is not impaired at low body temperatures in thirteen-lined ground squirrels (Bullard and Funkhauser, 1962). If, as in thirteen-lined ground squirrels (Bullard and Funkhauser, 1962), stroke volume in bats does not change significantly at low body temperatures then the percentage of injected 86-Rb remaining per unit volume of blood after a given number of heart beats should be similar at different body temperatures provided the isotope qualifies as a flow-limited substance at all body temperatures. This, however, is probably not quite true. Under conditions such that much of the blood is shunted through arterio-venous bypasses, a somewhat larger than expected amount of 86-Rb will remain in the blood. Ideally, the determination of the effect of temperature on the uptake of 86-Rb necessitates perfusion studies of all organs at various body temperatures. At present, this is technically not feasible. Therefore, and also because this study is concerned mainly with changes in the distribution of blood during arousal from hibernation rather than exact blood flow measurements, the index used is considered to be a sufficiently reliable one.

Graphs A and B (Fig. 19) denote the mean percentages of injected 86-Rb remaining per 1 ml of blood at two body temperatures and different intervals between 86-Rb and KCl (which stops the heart) injections. In the first experiment (Graph A) the isotope was injected during early arousal at a heart rate of 40 beats per minute, when the highest and lowest average body temperatures (recorded in other bats under similar conditions) were 6.2 C for the interscapular brown adipose tissue and 6.7 C for the colon (App. 5; Tables 1 and 4). In the second experiment

Fig. 19. Percentages of injected 86-Rb (Rubidium) remaining per 1 ml of blood of *E. fuscus*. The isotope was injected during early arousal from hibernation (T_a = 5 C) at a heart rate of 40 beats per minute (Graph A) or during the second half of arousal from hibernation (T_a = 5 C) at a heart rate of 480 beats per minute (Graph B). Sixty, 120, 240 and 480 heart beats passed between 86-Rb and KCl (which stops the heart) injections. Each point, except the last (heart beats = 480), represents the mean of 4 to 8 experiments. Height of vertical line at each point represents standard deviation.


A
B
16
12
8
4
0
120
240
360
480
PERCENTAGE OF INJECTED 86-Rb
REMAINING PER 1 ml OF BLOOD
NUMBER OF HEART BEATS
BETWEEN 86-Rb AND KCl INJECTIONS

(Graph B), the isotope was injected during the second half of arousal at a heart rate of 480 beats per minute when the highest and lowest temperatures were 29.8 C for the interscapular brown adipose tissue and 14.2 C for the colon. As indicated, 60, 120, 240, and 480 heart beats passed between 86-Rb and KCl injections. Although the amount of 86-Rb per unit volume of blood at each of the measured points is slightly higher in early arousal (Table VII; individual values: App. 3, Tables 1 and 2), differences are not statistically significant (Table VIII). A similar stroke volume at heart rates 40 and 480 beats per minute but a higher blood flow through arterio-venous shunts during early arousal could account for the difference. Since at both heart rates the amount of 86-Rb per unit volume differs least when 120 heart beats follow the rubidium injection, this number of heart beats determined the interval between isotope and KCl injections in subsequent studies.

That 86-Rb is a flow-limited rather than time-limited capillary flow indicator is also demonstrated by comparing certain data from the preliminary studies and the subsequent arousal studies (Fig. 20). With a constant time interval, 60 seconds, between isotope and KCl injections (Graph D), the amount of 86-Rb remaining per unit volume of blood declines considerably at the higher heart rates during the arousal process (Table IX; individual values: App. 3, Tables 3 and 4). This is what one would expect. On the other hand, if cardiac output is the same (120 heart beats at a constant SV) between isotope and KCl injections (Graph C), then, provided 86-Rb is a flow-limited substance at all body temperatures, the amount of rubidium per unit volume of blood should be similar at all heart rates during arousal (Table IX). Statistical analysis (Table X)

Table VII. Percentages (%) of injected 86-Rb (Rubidium) remaining per 1 ml of blood of *E. fuscus*, sacrificed at heart rates 40 beats per minute (Graph A; Fig. 19) and 480 beats per minute (Graph B; Fig. 19) during the arousal from hibernation (T_a = 5 C). Sixty, 120, 240, and 480 heart beats passed between 86-Rb and KCl injections.

Number of heart beats between 86-Rb and KCl injections	Percentage of injected 86-Rb remaining per 1 ml of blood				Number of animals in each group
	E. fuscus sacrificed at HR = 40 beats per minute (Graph A; Fig. 19)		*E. fuscus* sacrificed at HR = 480 beats per minute (Graph B; Fig. 19)		
	Mean	s_d (±)	Mean	s_d (±)	
60	15.53	2.51	14.60	2.72	4
120	10.37	0.86	9.35	1.15	8
240	8.05	1.04	7.62	0.49	6
480	4.50		4.43		1

Table VIII. Results from statistical analysis (Student-Newman-Keuls procedure) on percentages (%) of injected 86-Rb (Rubidium) remaining per 1 ml of blood of *E. fuscus*, sacrificed at heart rates 40 beats per minute (Graph A; Fig. 19) and 480 beats per minute (Graph B; Fig. 19) during the arousal from hibernation (T_a = 5 C). Sixty, 120, 240, and 480 heart beats passed between 86-Rb and KCl injections.

60 heart beats between 86-Rb and KCl injections (Graphs A and B; Fig. 19)	A	120 heart beats between 86-Rb and KCl injections (Graphs A and B; Fig. 19)	A
	B		B
240 heart beats between 86-Rb and KCl injections (Graphs A and B; Fig. 19)	A		
	B		

A: refers to the mean percentage of injected 86-Rb remaining per 1 ml of blood of *E. fuscus*, sacrificed at a heart rate of 40 beats per minute during the arousal from hibernation (T_a = 5 C).

B: refers to the mean percentage of injected 86-Rb remaining per 1 ml of blood of *E. fuscus*, sacrificed at a heart rate of 480 beats per minute during the arousal from hibernation (T_a = 5 C).

Fig. 20. Percentages of injected 86-Rb (Rubidium) remaining per 1 ml of blood of *E. fuscus*. In one set of experiments (Graph C), the isotope was injected during deep hibernation (HR = 12 beats/min; T_a = 5 C) and at different heart rates during the arousal from hibernation (T_a = 5 C). One hundred and twenty heart beats passed between 86-Rb and KCl (which stops the heart) injections. Each point represents the mean of 6 to 8 experiments. Height of vertical line at each point represents standard deviation. In the other set of experiments (Graph D), the isotope was injected at different heart rates during the arousal from hibernation (T_a = 5 C). Sixty seconds passed between 86-Rb and KCl injections. Each point represents 1 experiment.

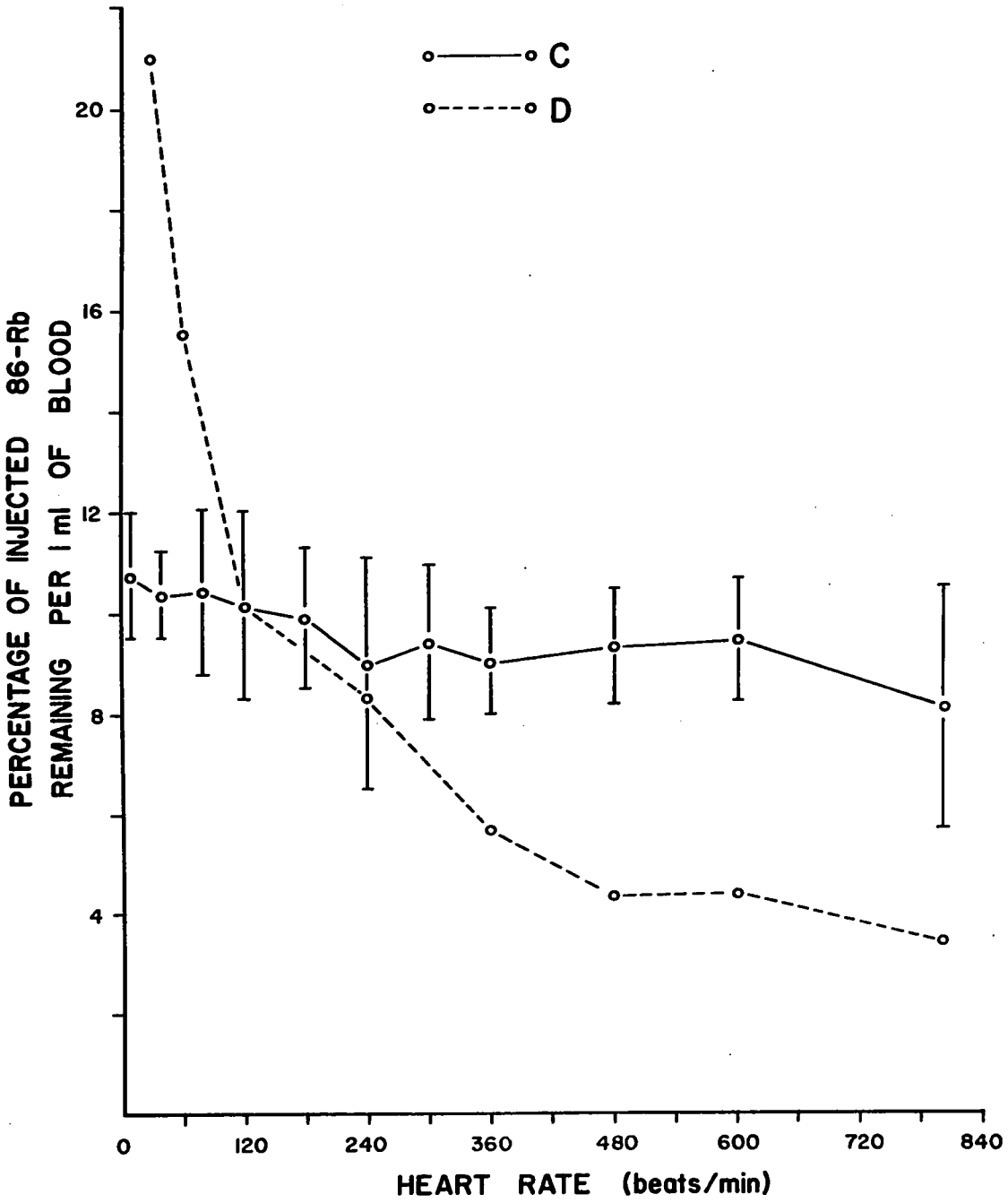

C
D
20
16
12
8
4
PERCENTAGE OF INJECTED 86-Rb
REMAINING PER 1 ml OF BLOOD
0
120
240
360
480
600
720
840
HEART RATE (beats/min)

Table IX. Percentages (%) of injected 86-Rb (Rubidium) remaining per 1 ml of blood of *E. fuscus*, sacrificed during deep hibernation (HR = 12 beats/min) and at different heart rates during the arousal from hibernation (T_a = 5 C). In one set of experiments (Graph C; Fig. 20), 120 heart beats passed between 86-Rb and KCl injections. In the other set of experiments (Graph D; Fig. 20), 60 seconds passed between 86-Rb and KCl injections.

120 heart beats between 86-Rb and KCl injections (Graph C; Fig. 20)				60 seconds between 86-Rb and KCl injections (Graph D; Fig. 20)		
E. fuscus sacrificed at heart rates (beats/min)	Percentage 86-Rb per 1 ml blood		Number of animals	*E. fuscus* sacrificed at heart rates (beats/min)	Percentage 86-Rb per 1 ml blood	Number of animals
	Mean	s_d (±)			Mean	
12	10.74	1.26	6			
40	10.37	0.86	8	20	21.05	1
80	10.43	1.64	8	60	15.57	1
120	10.14	1.88	8	120	10.45	1
180	9.85	1.41	8			
240	8.84	2.36	8	240	8.47	1
300	9.41	1.56	8			
360	9.03	1.10	8	360	5.69	1
480	9.36	1.14	8	480	4.38	1
600	9.51	1.24	8	600	4.42	1
800	8.11	1.55	8	800	3.63	1

Table X. Results from statistical analysis (Student-Newman-Keuls procedure) on percentages (%) of injected 86-Rb (Rubidium) remaining per 1 ml of blood of *E. fuscus*, sacrificed in deep hibernation (HR = 12 beats/min; T_a = 5 C), at different heart rates during the arousal from hibernation (T_a = 5 C), and during a post-arousal (HR = 480 beats/min; T_a = 22 C), resting state (Graph C; Fig. 20).

A statistical comparison is also presented for the percentages of injected 86-Rb remaining per 1 ml of blood of non-hibernating (HR = 335 beats/min; T_a = 22 C), deeply hibernating (HR = 12 beats/min; T_a = 5 C), and post-arousal (HR = 480 beats/min; T_a = 22 C) bats. In all experiments, 120 heart beats passed between 86-Rb and KCl injections.

E. fuscus sacrificed at heart rates (beats/min)	Percentage 86-Rb per 1 ml blood Mean		*E. fuscus* sacrificed at heart rates (beats/min)	Percentage 86-Rb per 1 ml blood Mean
DH-W 12	10.74	I		
A-W 80	10.43	I	DH-W 12	10.74
A-W 40	10.37	I		
A-W 120	10.14	I	A-NH 335	10.69
A-W 180	9.85	II		
A-W 600	9.51	II	PA-W 480	9.46
PA-W 480	9.46	II		
A-W 480	9.36	II		
A-W 360	9.03	II		
A-W 240	8.84	II		
A-W 800	8.11	I		

(Graph C; Fig. 20)

A-NH: refers to the mean percentage of injected 86-Rb remaining per 1 ml of blood of *E. fuscus*, sacrificed in a non-hibernating, lightly anaesthetized state in the summer.

DH-W: refers to the mean percentage of injected 86-Rb remaining per 1 ml of blood of *E. fuscus*, sacrificed in deep hibernation in the winter.

A-W: refers to the mean percentage of injected 86-Rb remaining per 1 ml of blood of *E. fuscus*, sacrificed during the arousal from hibernation in the winter.

PA-W: refers to the mean percentage of injected 86-Rb remaining per 1 ml of blood of *E. fuscus*, sacrificed in a post-arousal (resting) state in the winter.

shows that this is the case for all values obtained except for that during peak arousal (HR = 800 beats/min). However, since this value (8.11% 86-Rb/ml blood) is not significantly different from the lower values obtained at other heart rates during arousal, the one value (8.11% 86-Rb/ml blood) does not disprove that 86-Rb is a flow-limited capillary indicator at all body temperatures. A comparison among the amounts of 86-Rb remaining per unit volume of blood of deeply hibernating, arousing, post-arousal, and non-hibernating bats shows no statistically significant differences. In all of these experiments, 120 heart beats passed between 86-Rb and KCl injections. Therefore, the 86-Rb method was accepted as a valid method for measuring the distribution of blood in bats during different physiological states.

DISTRIBUTION OF BLOOD

1. Hibernating Bats

The distribution of blood in various organs and tissues of deeply hibernating *E. fuscus* is depicted in Figure 21. Mean values and results of statistical analysis are presented in Tables XI and XII. Individual values are listed in Appendix 4, Tables 2 and 3. The percentage of 86-Rb taken up per organ or tissue corresponds closely to the percentage of cardiac output delivered to that organ or tissue (Sapirstein, 1958).

A most conspicuous finding in this study is the proportionality with which cardiac output is distributed among a variety of organs and tissues of deeply hibernating bats. In the first study carried out during the winter, the percentage of cardiac output received by muscle, diaphragm, kidneys, liver and stomach (Table XI) approximates the

percentage lean weights (Table V) of these organs. The relationship is similar for brown fat, though this tissue is expressed in terms of semi-lean body weight. In contrast, the percentages of cardiac output delivered to myocardium, intestine, carcass, and skin approximate 3.0, 1.50, 0.66, and 0.5 times that of their percentage lean body weights, respectively. White adipose tissue, which comprises about 1/5 of the total body weight, receives less than 1/20 of the cardiac output. In terms of work load, it is not surprising that the myocardium receives the greatest relative fraction of the cardiac output, neither unexpected is the extremely low value for white adipose tissue, its scanty vascularization implying a relatively limited blood supply under any physiological condition. The relative fraction of cardiac output received by the skin is lower than that of any organ except white fat, but under such conditions as anaesthesia (Table XIX), the skin receives twice the fraction as during hibernation. This finding, not demonstrated previously, is considered important in that it offers partial explanation for the core temperature of a hibernator being above that of the environment during deep hibernation when other thermoregulatory responses are apparently absent (Hammel, 1968). Finally, it is noteworthy that the wings comprise about 1/5 the weight of what is referred to as carcass. A relatively low fraction of cardiac output delivered to the wings could contribute to the relatively low percentage of 86-Rb received by the carcass.

The same general relationships are found when comparing the percentages of cardiac output received by organs and tissues to the percentage weights of these organs and tissues of bats placed into the

cold (T_a = 5 C) during the summer (Fig. 21; Tables XI and XII). However, in some cases this relationship does not hold. Whereas the differences in the fractions of radioactive rubidium received by posterior muscle, brown adipose tissue, and white adipose tissue in the two groups of bats correspond directly to the percentage weight differences of these tissues (Table V), the higher fractions of cardiac output delivered to the myocardium, skin and carcass of bats placed into the cold during the summer are not reflections of percentage weight differences. Our present understanding of the phenomena associated with hibernation cannot explain these findings, although the assumption may be made that the high mortality rate (Section: Materials and Methods) within this group of bats is a consequence of their inability to sufficiently reduce blood flow to skin and presumably of a dysfunction of the kidneys. Haematuria (blood in urine) was observed frequently in these experimental animals. Furthermore, Rosenbaum *et al.* (1967) demonstrated morphological differences among kidney tissue slices from non-hibernating *M. lucifugus*, from those that hibernated during the summer, and from bats that hibernated in the winter. Thickness of the proximal convoluted renal tubular epithelium, size of epithelial cells and microvilli of the brush border as well as the vacuolar complex were grossly different in tissues from non-hibernating bats as compared to those hibernating in the winter. Morphological changes in kidney tissue were of an intermediary nature in animals placed into the cold during the summer. The administration of antidiuretic hormone (ADH) induced winter-like changes in bats subjected to cold (T_a = 4 C) during the summer. Menaker (1962), who found seasonal variations in the ability of *M. lucifugus* to arouse from hibernation,

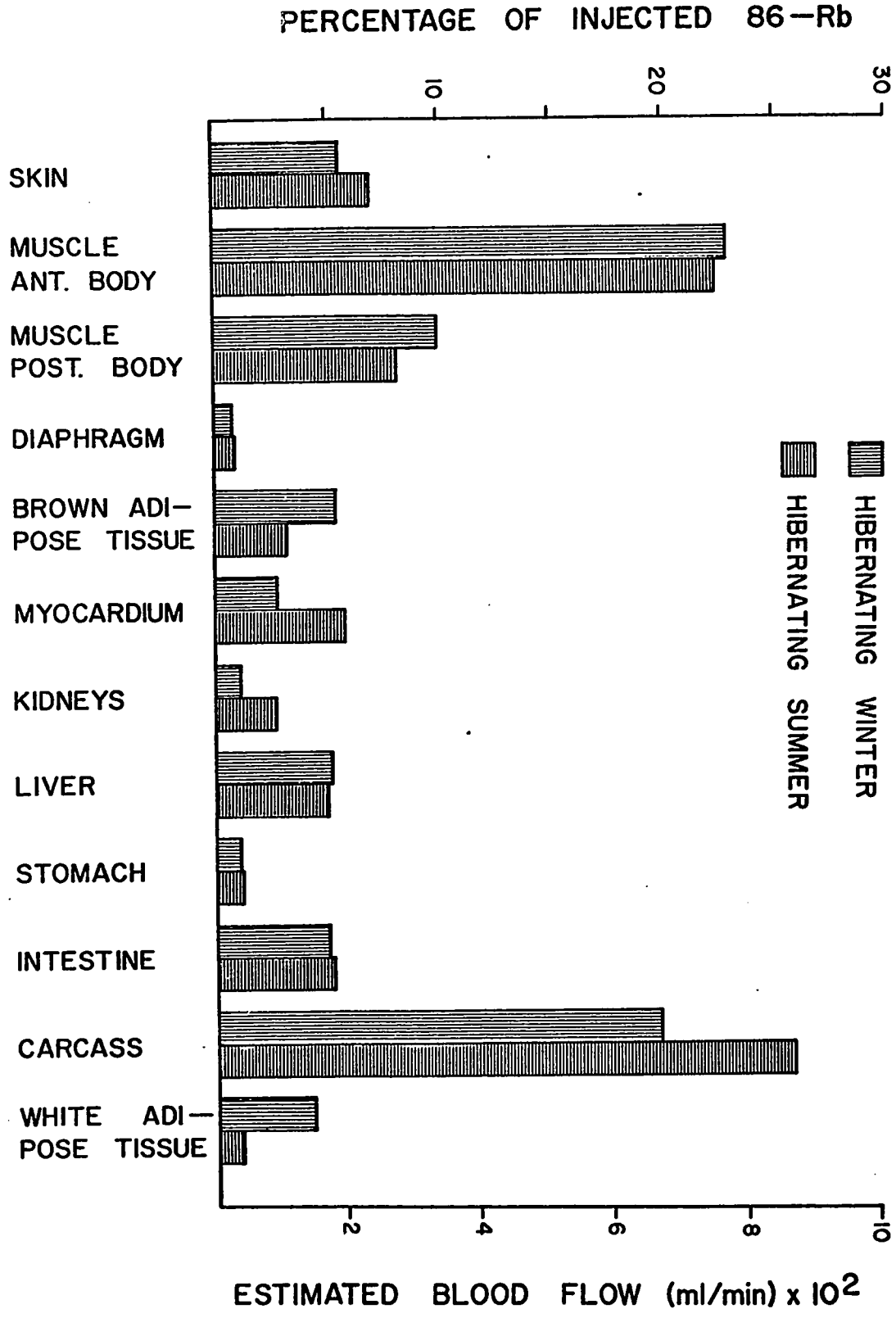

PERCENTAGE OF INJECTED 86—Rb
10
20
30
SKIN
MUSCLE ANT. BODY
MUSCLE POST. BODY
DIAPHRAGM
BROWN ADI—POSE TISSUE
MYOCARDIUM
KIDNEYS
LIVER
STOMACH
INTESTINE
CARCASS
WHITE ADI—POSE TISSUE
HIBERNATING WINTER
HIBERNATING SUMMER
2
4
6
8
10
ESTIMATED BLOOD FLOW (ml/min) x 10²

Table XI. Percentage of injected 86-Rb (Rubidium) per organ or tissue of *E. fuscus*, sacrificed during deep hibernation in the winter and in the summer.

	DEEP HIBERNATION (T_a = 5 C)			
	Winter		Summer	
Heart rate	12		12	
No. of animals	6		5	
Tissue or organ	Mean	s_d (±)	Mean	s_d (±)
Skin	5.70	0.55	6.98	0.70
Muscle ant. body	22.92	1.08	22.24	3.65
Muscle post. body	9.98	0.51	8.11	1.30
Total muscle	32.91	0.92	30.35	4.78
Diaphragm	0.72	0.08	0.91	0.07
Interscap. B.A.T.	2.63	0.38	1.65	0.47
Other B.A.T.	2.60	0.50	1.57	0.38
Total B.A.T.	5.23	0.85	3.22	0.84
Liver	5.13	0.56	5.00	1.01
Kidneys	1.22	0.28	2.74	0.84
Stomach	1.14	0.30	1.20	0.20
Intestine	5.15	0.79	5.21	1.61
Myocardium	2.75	0.44	5.85	0.63
Blood	15.24	1.73	11.41	1.81
W.A.T.	4.25	2.13	1.08	0.62
Carcass	20.54	1.19	26.05	0.89

Table XII. Results from statistical analysis (Student-Newman-Keuls procedure) on percentages (%) of injected 86-Rb (Rubidium) per organ or tissue of *E. fuscus*, sacrificed during deep hibernation (HR = 12 beats/min; T_a = 5 C) in the winter and in the summer.

Skin:	DH-S DH-W	Muscle ant. body:	DH-W DH-S	Muscle post. body:	DH-W DH-S	Total muscle:	DH-W DH-S
Diaphragm:	DH-S DH-W	Interscap. B.A.T.:	DH-W DH-S	Other B.A.T.:	DH-W DH-S	Total B.A.T.:	DH-W DH-S
Liver:	DH-W DH-S	Kidneys:	DH-S DH-W	Stomach:	DH-S DH-W	Intestine:	DH-S DH-W
Myocardium:	DH-S DH-W	W.A.T.:	DH-W DH-S	Carcass:	DH-S DH-W		

DH-W: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed during deep hibernation in the winter.

DH-S: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed during deep hibernation in the summer.

suggested differences in circulatory adaptations, and hence in heat loss, between bats placed into the cold in winter and in summer. The present study demonstrates a higher fraction of cardiac output and therefore a higher blood flow to skin, and presumably also to wings (higher value for carcass) in bats hibernating during the summer. However, peripheral blood vessels of these animals are not dilated maximally as evidenced by values obtained during anaesthesia (Table XIX). The amount of extra heat loss, due to higher circulation to the skin of bats in the cold during the summer over those hibernating in the winter has not been quantified even though such measurements might yield valuable information about the role of the circulatory system in preventing heat loss during hibernation.

2. Arousing Bats

Mean values (Tables XIII and XIV) were used in delineating the sequential changes in the fractional delivery of cardiac output to various organs and tissues of *E. fuscus* during the arousal from hibernation in the winter (Figs. 22 and 23) and in the summer (Figs. 24 and 25). Individual values of the fractions of cardiac output received by various organs and tissues (percentage of injected 86-Rb) of bats and results from statistical analysis are presented in Appendices 4 and 6, respectively.

In constructing graphs, values for the X-axis showing heart rates during arousal were taken from experiments described earlier in this section. They represent integrated means of 20 studies performed during the summer and 20 studies performed during the winter (App. 1; Tables 2 and 3). After plotting mean values for percentage organ uptake of injected 86-Rb (Y-axis) against heart rates during arousal (X-axis), graphs were obtained by drawing the curve of apparent best fit for all points.

Fig. 22. Sequential changes in the distribution of blood in *E. fuscus* during the arousal from hibernation (T_a = 5 C) in the winter. Percentage of injected 86-Rb (Rubidium) per organ or tissue represents percentage of cardiac output received by that organ or tissue (Sapirstein, 1958). Measurements were made at different heart rates (Table XIII) during arousal. Graphs were obtained by plotting mean values for percentage organ uptake of injected 86-Rb and drawing the curves of apparent best fit for all points. Mean values, standard deviations and number of measurements are presented in Table XIII.

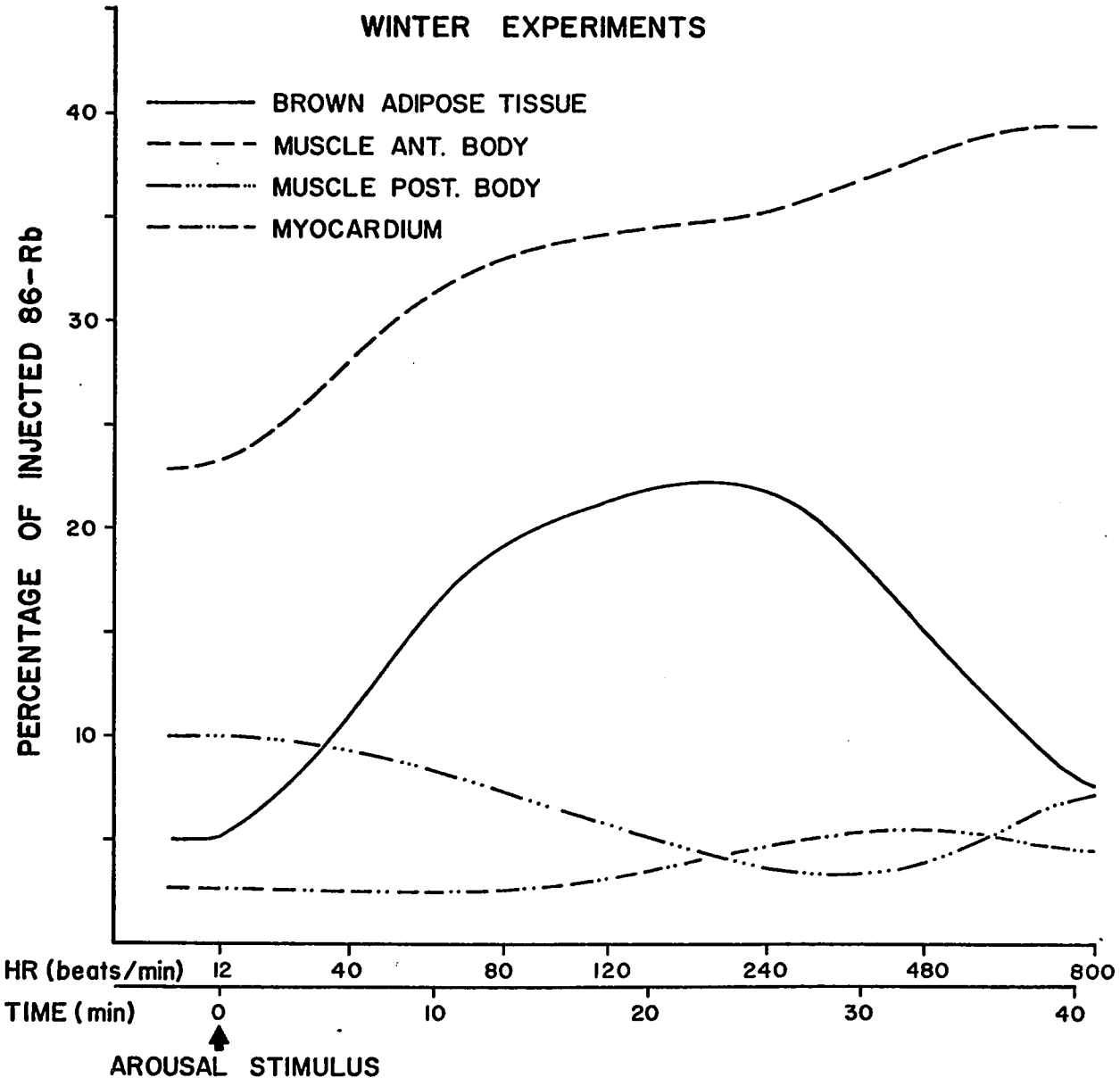

WINTER EXPERIMENTS
BROWN ADIPOSE TISSUE
MUSCLE ANT. BODY
MUSCLE POST. BODY
MYOCARDIUM
PERCENTAGE OF INJECTED 86-Rb
40
30
20
10
HR (beats/min) 12 40 80 120 240 480 800
TIME (min) 0 10 20 30 40
AROUSAL STIMULUS

Fig. 23. Sequential changes in the distribution of blood in *E. fuscus* during the arousal from hibernation (T_a = 5 C) in the winter. Percentage of injected 86-Rb (Rubidium) per organ or tissue represents percentage of cardiac output received by that organ or tissue (Sapirstein, 1958). Measurements were made at different heart rates (Table XIII) during arousal. Graphs were obtained by plotting mean values for percentage organ uptake of injected 86-Rb and drawing the curves of apparent best fit for all points. Mean values, standard deviations and number of measurements are presented in Table XIII.

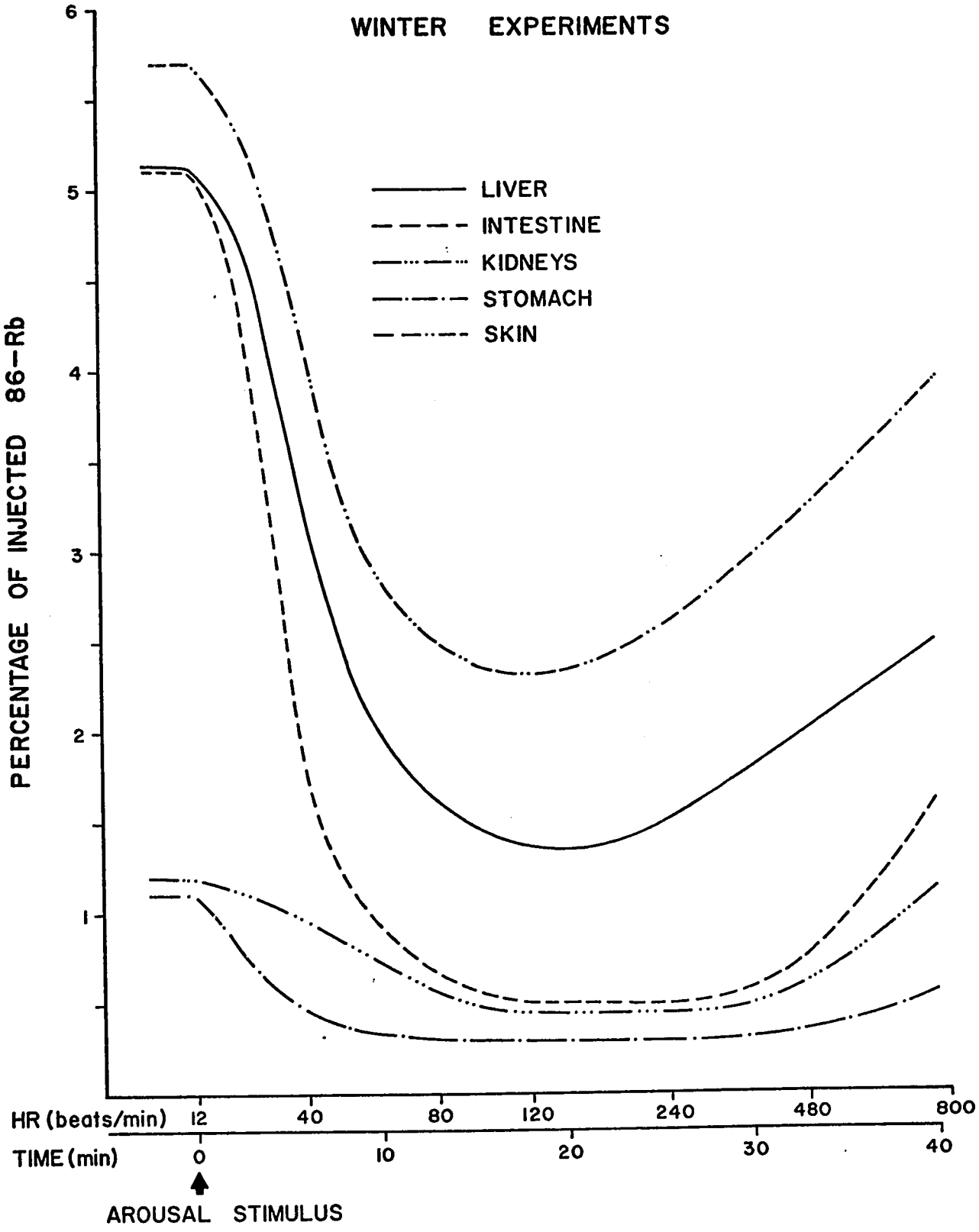

WINTER EXPERIMENTS
LIVER
INTESTINE
KIDNEYS
STOMACH
SKIN
PERCENTAGE OF INJECTED 86-Rb
6
5
4
3
2
1
HR (beats/min) 12 40 80 120 240 480 800
TIME (min) 0 10 20 30 40
AROUSAL STIMULUS

Table XIII. Percentage of injected 86-Rb (Rubidium) per organ or tissue of from hibernation in the winter.

AROUSAL FROM HIBERNATION

HR No. of animals	40 8		80 8		120 8		180 8	
Tissue or organ	Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)
Skin	3.24	0.55	2.74	0.22	2.39	0.37	3.06	0.65
Muscle ant. body	34.28	2.16	29.35	1.38	34.72	1.96	32.88	2.25
Muscle post. body	9.53	0.48	7.15	1.45	6.63	0.70	4.61	0.89
Total muscle	43.81	2.25	36.50	2.73	41.34	1.98	37.49	1.97
Diaphragm	0.75	0.09	0.72	0.09	0.72	0.16	0.76	0.15
Interscap. B.A.T.	5.41	1.82	12.36	1.72	10.14	2.31	11.67	1.27
Other B.A.T.	4.88	1.44	8.73	1.63	9.08	1.59	9.14	1.44
Total B.A.T.	10.29	3.13	21.09	3.32	19.22	3.61	20.81	1.67
Liver	2.37	0.59	2.12	0.29	2.06	0.69	1.34	0.25
Kidneys	0.52	0.07	0.62	0.12	0.44	0.10	0.41	0.07
Stomach	0.38	0.18	0.32	0.06	0.28	0.03	0.31	0.06
Intestine	0.98	0.35	0.89	0.40	0.50	0.08	0.53	0.04
Myocardium	2.37	0.51	2.83	0.44	3.33	0.45	4.51	0.50
Blood	16.38	1.53	15.69	3.41	13.89	1.90	12.99	1.21
W.A.T.	1.96	0.45	1.82	0.36	1.62	0.38	1.55	0.73
Carcass	17.07	1.55	14.67	1.30	14.22	1.76	16.22	1.45

E. fuscus, sacrificed at different heart rates (HR) during the arousal

(T_a = 5 C) IN WINTER

240 8		300 8		360 8		480 8		600 8	
Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)
2.52	0.32	2.59	0.46	2.80	0.61	2.59	0.42	4.12	0.50
34.78	2.25	33.14	3.56	36.48	3.20	37.10	2.77	38.89	1.98
4.04	0.46	4.97	1.19	4.26	1.11	2.94	0.62	4.39	0.60
38.81	2.31	38.11	3.87	40.72	2.93	40.04	3.00	43.28	2.21
0.82	0.15	0.86	0.32	0.95	0.23	0.97	0.24	0.84	0.16
13.74	2.54	11.01	3.20	9.39	2.18	9.60	1.99	7.16	0.86
10.40	2.50	9.47	2.78	7.67	1.50	7.95	1.77	5.74	0.69
24.13	4.55	20.47	5.79	17.07	3.36	17.59	3.58	12.91	1.34
1.27	0.40	1.58	0.47	1.60	0.40	1.80	0.61	1.92	0.69
0.48	0.23	0.51	0.13	0.42	0.14	0.70	0.10	0.41	0.09
0.28	0.04	0.31	0.12	0.34	0.11	0.38	0.12	0.38	0.16
0.51	0.10	0.50	0.17	0.62	0.20	0.83	0.25	0.58	0.19
4.13	0.40	4.90	0.91	4.85	0.81	5.78	0.68	4.82	0.43
12.40	2.80	13.21	2.20	13.31	1.98	13.68	1.83	12.57	1.60
1.50	0.51	1.84	0.78	1.34	0.74	1.13	0.49	1.76	0.49
13.14	1.52	15.11	2.30	15.97	1.35	14.51	2.53	16.40	0.91

Table XIII (continued)

AROUSAL FROM HIBERNATION (T_a = 5 C) IN WINTER

HR	800	
No. of animals	8	
Tissue or organ	Mean	s_d (±)
Skin	3.31	0.49
Muscle ant. body	39.42	2.57
Muscle post. body	7.21	1.60
Total muscle	46.63	3.46
Diaphragm	0.96	0.23
Interscap. B.A.T.	5.00	1.30
Other B.A.T.	4.42	1.27
Total B.A.T.	9.42	2.49
Liver	2.48	0.43
Kidneys	1.21	0.81
Stomach	0.54	0.19
Intestine	1.63	0.89
Myocardium	4.76	0.53
Blood	10.78	1.09
W.A.T.	2.22	
Carcass	16.26	1.84

Values to the left of zero time (X-axis), the instant when arousal stimulus was applied, refer to the percentage organ uptake of 86-Rb and thus to the fraction of cardiac output received by these organs during deep hibernation.

Plots of data from winter experiments (Figs. 22 and 23) demonstrate that redistribution of blood starts immediately following the initiation of arousal from hibernation. Typically, there is a marked increase in the fractions of cardiac output delivered to brown adipose tissue and anterior muscle, and a corresponding decrease in the fractions of cardiac output received by skin, abdominal organs and posterior muscle during early arousal as compared to deep hibernation. These are gradual, progressive shifts toward maximum and minimum values. Myocardium and diaphragm are exceptional in that the percentage of cardiac output received does not change significantly until near mid-arousal, when a heart rate of about 120 beats per minute is attained. At about this time, brown fat receives its largest and skin and abdominal organs their lowest proportion of the cardiac output. Except for myocardium and posterior muscle, the fractions of cardiac output delivered to various organs are fairly stable between heart rates of 120 to 240 beats per minute. Subsequently, values for brown fat start to decline and those for anterior muscle, skin, and liver begin to rise. The myocardium obtains its largest fraction of cardiac output considerably later in arousal than brown fat, but much earlier than the other tissues and organs. Definite increments in the percentages of cardiac output delivered to visceral organs and posterior muscle do not become evident until late arousal, at heart rates of about 360 to 480 beats per minute. Henceforth, all organs and tissues other than the

myocardium and brown fat receive rapidly increasing fractions of cardiac output. There are no significant changes in the fractions of cardiac output received by the myocardium and brown adipose tissue between peak arousal and post-arousal states. On the other hand, while the fractional delivery of cardiac output to anterior muscle declines during the period when the heart rate is in this range, the fractions to the abdominal viscera, posterior muscle, and skin increase significantly during this period (Tables XIII and XIV; App. 6).

Differences in the times required for arousal from induced hibernation in the summer and from a more natural hibernation in the winter have been illustrated earlier (Figs. 1 and 2). These differences (Figs. 22 to 25) are associated with both differences in the relative percentage weights of brown adipose tissue (Tables V and VI), and alterations in circulation (Tables XIII and XIV). Although general trends in circulation appear similar in the two groups of arousing bats, a considerably lower percentage of the cardiac output is delivered to brown adipose tissue and a significantly higher fraction goes to the skin of bats arousing during the summer. Brown adipose tissue has a high thermogenic capacity (review: Lindberg, 1970), which is evoked maximally under such conditions as arousal from hibernation (Hayward and Lyman, 1967). In addition, a relationship exists between blood flow and the metabolic activity of a tissue (Honig, 1968), and peripheral vasoconstriction reduces heat loss to a cold environment (Berne and Levy, 1967). Consequently, the findings suggest reduced contribution of heat by brown fat to the overall thermogenesis and increased heat loss to the environment as a consequence of a higher blood flow to the skin during

Fig. 24. Sequential changes in the distribution of blood in *E. fuscus* during the arousal from hibernation (T_a = 5 C) in the summer. Percentage of injected 86-Rb (Rubidium) per organ or tissue represents percentage of cardiac output received by that organ or tissue (Sapirstein, 1958). Measurements were made at different heart rates (Table XIV) during arousal. Graphs were obtained by plotting mean values for percentage organ uptake of injected 86-Rb and drawing the curves of apparent best fit for all points. Mean values, standard deviations and number of measurements are presented in Table XIV.

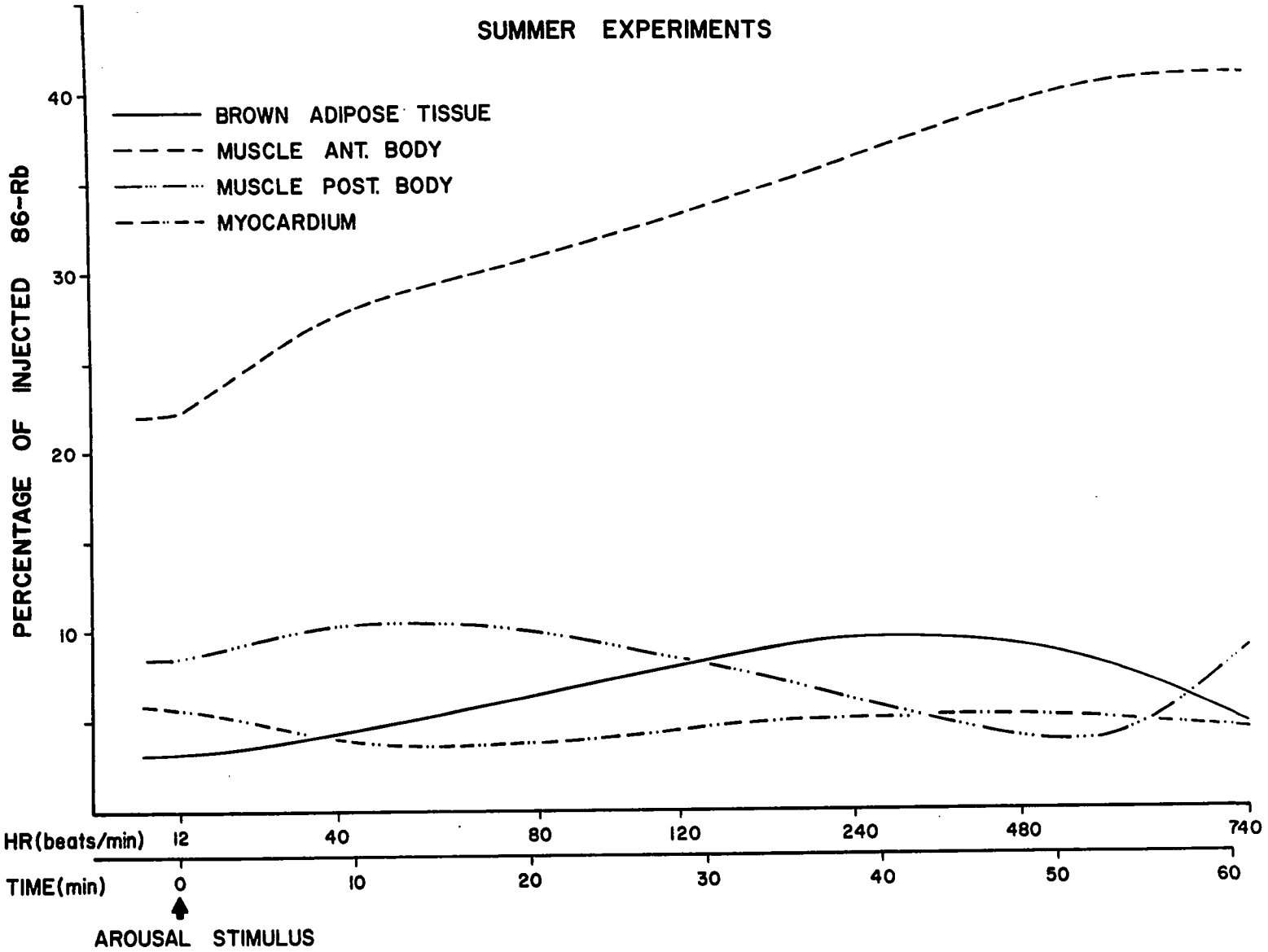

SUMMER EXPERIMENTS
BROWN ADIPOSE TISSUE
MUSCLE ANT. BODY
MUSCLE POST. BODY
MYOCARDIUM
PERCENTAGE OF INJECTED 86-Rb
40
30
20
10
HR(beats/min)
12
40
80
120
240
480
740
TIME(min)
0
10
20
30
40
50
60
AROUSAL STIMULUS

Fig. 25. Sequential changes in the distribution of blood in *E. fuscus* during the arousal from hibernation (T_a = 5 C) in the summer. Percentage of injected 86-Rb (Rubidium) per organ or tissue represents percentage of cardiac output received by that organ or tissue (Sapirstein, 1958). Measurements were made at different heart rates (Table XIV) during arousal. Graphs were obtained by plotting mean values for percentage organ uptake of injected 86-Rb and drawing the curves of apparent best fit for all points. Mean values, standard deviations and number of measurements are presented in Table XIV.

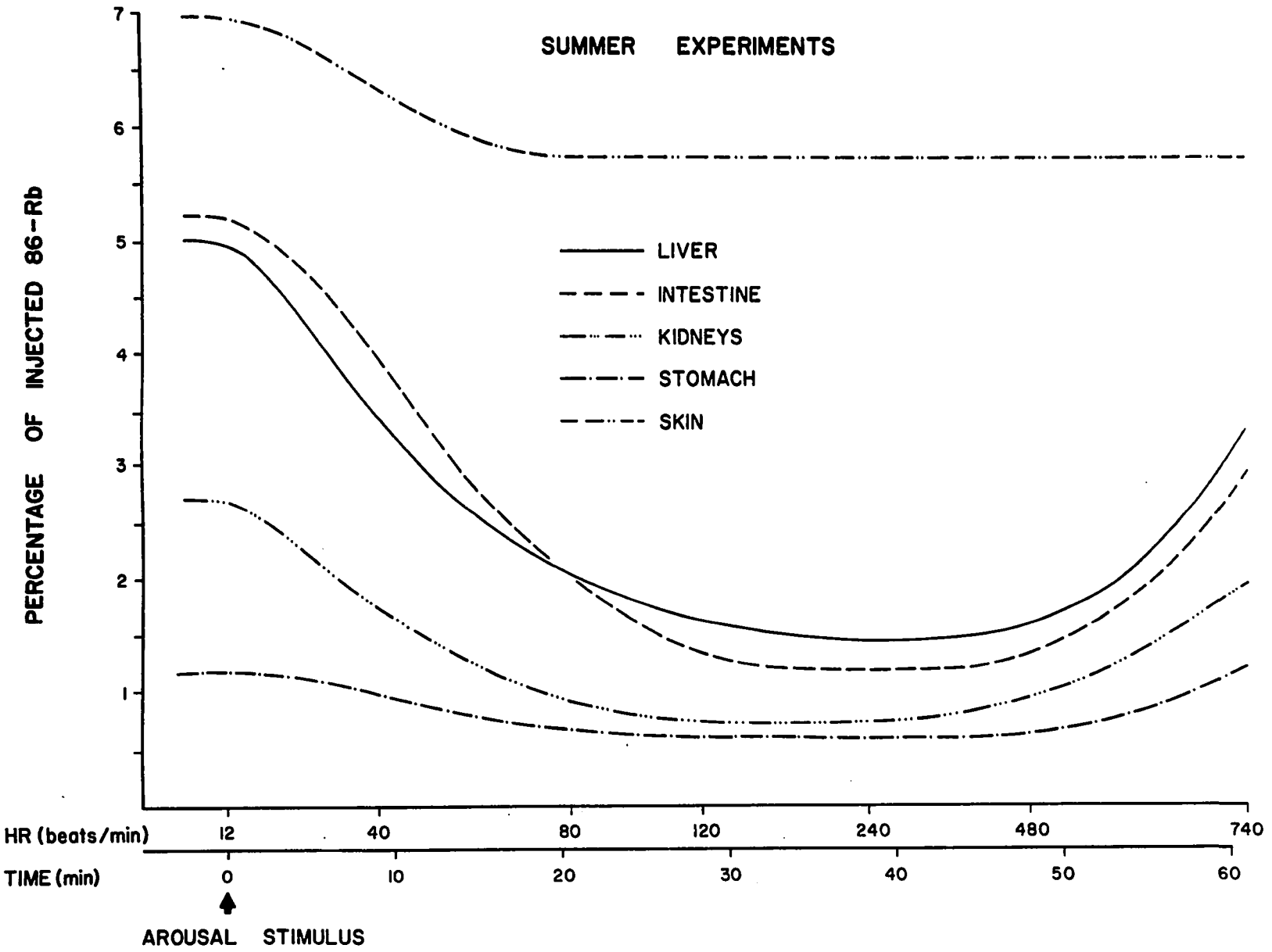

SUMMER EXPERIMENTS
PERCENTAGE OF INJECTED 86-Rb
7
6
5
4
3
2
1
LIVER
INTESTINE
KIDNEYS
STOMACH
SKIN
HR (beats/min)
12
40
80
120
240
480
740
TIME (min)
0
10
20
30
40
50
60
AROUSAL STIMULUS

Table XIV. Percentage of injected 86-Rb (Rubidium) per organ or tissue of from hibernation in the summer.

AROUSAL FROM HIBERNATION

HR No. of animals	40 4		80 4		120 5		180 4	
Tissue or organ	Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)
Skin	5.43	0.56	6.13	1.05	6.30	1.80	5.05	1.38
Muscle ant. body	27.90	3.00	34.12	4.55	30.35	3.74	37.45	3.21
Muscle post. body	10.18	2.71	11.29	2.62	6.50	2.21	10.13	1.71
Total muscle	38.08	5.34	45.41	6.66	36.85	5.17	47.58	4.50
Diaphragm	1.17	0.15	0.94	0.21	0.91	0.16	0.92	0.36
Interscap. B.A.T.	3.33	1.38	2.34	1.15	5.06	1.58	4.08	0.82
Other B.A.T.	2.20	0.79	1.99	0.54	4.34	1.29	3.86	0.69
Total B.A.T.	5.53	2.10	4.33	1.66	9.42	2.85	7.93	1.49
Liver	3.16	0.32	2.45	1.15	3.31	0.75	1.34	0.31
Kidneys	1.54	0.60	1.09	0.63	0.85	0.26	0.88	0.23
Stomach	1.00	0.24	1.11	0.54	0.66	0.30	0.46	0.09
Intestine	4.36	2.58	2.19	0.92	1.13	0.38	0.76	0.12
Myocardium	3.46	0.91	3.36	0.26	5.28	0.73	3.82	0.89
Blood	13.79	1.51	11.51	2.19	14.71	1.36	10.26	1.40
W.A.T.	0.75	0.58	1.17	0.27	0.88	0.31	0.85	0.33
Carcass	21.73	1.93	20.31	2.81	19.70	1.37	20.16	3.07

E. fuscus, sacrificed at different heart rates (HR) during the arousal

(T_a = 5 C) IN SUMMER

240 5		360 4		480 5		600 4		740 5	
Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)
4.34	1.46	4.89	2.13	6.67	0.87	4.38	1.20	4.57	0.97
37.74	0.64	38.11	1.75	39.08	3.41	41.18	3.75	41.35	3.14
7.48	0.78	5.78	0.76	4.82	1.56	3.74	0.40	8.68	0.76
45.22	0.93	43.89	1.34	43.90	2.81	44.92	3.82	50.03	3.94
0.99	0.10	0.85	0.04	0.94	0.14	0.73	0.08	0.78	0.16
4.76	1.48	5.83	1.51	4.31	1.08	5.19	0.60	2.62	0.58
4.24	1.65	4.82	1.35	3.33	1.30	4.20	0.56	2.22	0.25
9.00	3.13	10.64	2.85	7.65	2.36	9.39	1.07	4.84	0.76
1.60	0.47	1.41	0.29	1.50	0.64	3.27	1.31	3.30	1.03
0.65	0.58	0.75	0.61	1.12	0.71	1.55	0.14	1.99	1.38
0.77	0.25	0.46	0.12	0.67	0.25	0.69	0.15	1.30	0.34
1.19	0.89	1.13	0.70	1.48	1.08	1.69	0.41	3.02	1.85
4.89	0.59	5.02	0.52	5.03	1.39	4.71	0.67	4.35	0.80
12.54	1.70	11.61	1.64	10.86	1.96	10.54	0.95	10.15	1.30
0.94	0.55	1.36	0.59	0.88	0.65	1.05	0.59	1.05	0.69
17.82	2.17	17.98	1.48	19.28	1.89	17.08	1.70	14.61	1.95

summer arousal. Differences in the relative fractions of cardiac output received by brown adipose tissue are mainly, if not entirely, due to seasonal differences in the tissue's mass (Tables III to VI). However, since there are also seasonal changes in the animal's brown fat composition (Paulsrud and Dryer, 1968), partial differences due to altered metabolic demands for oxygen cannot be excluded. The higher fractional uptake of 86-Rb by the skin during arousal in the summer as compared to that during the winter cannot be attributed to differences in the weights of this organ (Tables III to VI). It should be noticed that of all organs and tissues tested the skin of bats used in summer experiments shows the greatest fluctuations in 86-Rb uptake (App. 4; Table 3) and hence in the fractions of cardiac output delivered to it. Actual dates (not given in this thesis) for individual experiments clearly indicate that the uptake of 86-Rb by skin of arousing bats increased between early June and late July and decreased following the end of August. This finding corresponds in time with the observed increase and decrease in mortality rate (Section: Materials and Methods). Inasmuch as the factors underlying cutaneous vasoconstriction in bats have not been investigated, the mechanism of decreased vasoconstriction during arousal in the summer is only speculative. Alterations within the central nervous system, neurohumoral factors, and local or circulating vasoconstrictor substances are possibly involved. Whatever the mechanisms, they seem to shift seasonally and apparently cannot be induced by simply placing bats into a cold environment during the summer.

Differences between the two groups of bats in the distribution of blood are not only confined to brown adipose tissue and skin. Statistical

analysis (App. 6; Table 3) shows that the fractional delivery of cardiac output to the myocardium is significantly higher during early arousal in bats used in summer experiments. Above a heart rate of about 180 beats per minute, differences in the fractions of cardiac output received by this tissue are not statistically significant between bats arousing in the summer and in the winter. Similar occurrences pertain to kidneys and intestine except that differences became insignificant at a heart rate of about 240 to 360 beats per minute. Whereas the values for the liver are similar between the two groups of bats, those for the stomach of bats used in the summer experiments are significantly higher during the entire course of arousal.

3. Post-arousal (Resting) Bats

The distribution of blood in resting *E. fuscus* retained in the warm (T_a = 22 C) for approximately 1 hour following the arousal from hibernation (T_a = 5 C) during the winter and summer is depicted in Figure 26. Mean values and results from statistical analysis are presented in Tables XV and XVI. Values from individual experiments are shown in Appendix 4, Tables 2 and 3.

A striking observation was that, following the arousal from hibernation in winter, blood redistributes itself such that its general pattern closely resembles that of deeply hibernating bats (Tables XVII and XVIII). There are some exceptions to this generalization. The fractions of cardiac output delivered to brown adipose tissue and to kidneys are significantly higher and that to the intestine is significantly lower in post-arousal (resting) bats as compared to those in deep hibernation (Table XVIII). Considering such important functions as

glomerular filtration rate and the concentrating and excreting of urine, the relatively high fraction of cardiac output delivered to the kidneys is to be expected, particularly following arousal from hibernation when catabolic waste products must be present in large amounts. On the other hand, the high value for brown fat suggests that the tissue's heat production is still of paramount importance during post-arousal conditions. Presumably, this value would decline considerably if the body temperature of the resting bats should again decrease to near that of the environment.

Comparing post-arousal conditions in summer and winter (Fig. 26; Table XV), significant differences in the uptake of 86-Rb concern anterior muscle and brown adipose tissue (Table XVI). Considerably larger fractions of the cardiac output are delivered to anterior muscle, and smaller fractions to brown adipose tissue, of bats in a post-arousal state during the summer as compared to those in the winter. Significant differences at the 5 percent but not at the 1 percent level of probability between post-arousal (resting) bats in the summer and winter are found for the liver, intestine, and white adipose tissue. The distribution of blood in other organs and tissues of the two groups of bats shows no statistically significant differences. Probably, the most important finding is the relatively high and low fraction of cardiac output received by anterior muscle and brown adipose tissue of bats following the arousal process in the summer. It appears likely that during this season, when the relative mass of brown fat is small and particular metabolites have become depleted during such an energy demanding process as arousal from hibernation, much heat is derived from the metabolic

Fig. 26. Distribution of blood and estimated blood flow in post-arousal (resting; HR = 480 beats/min; T_a = 22 C) *E. fuscus* in the winter and in the summer. Percentage of injected 86-Rb (Rubidium) per organ or tissue represents percentage of cardiac output received by that organ or tissue (Sapirstein, 1958). The estimated blood flow rate is an approximation based on a constant theoretical stroke volume of 0.024 ml (Section: Materials and Methods). Mean values, standard deviations and number of measurements are presented in Table XVII.

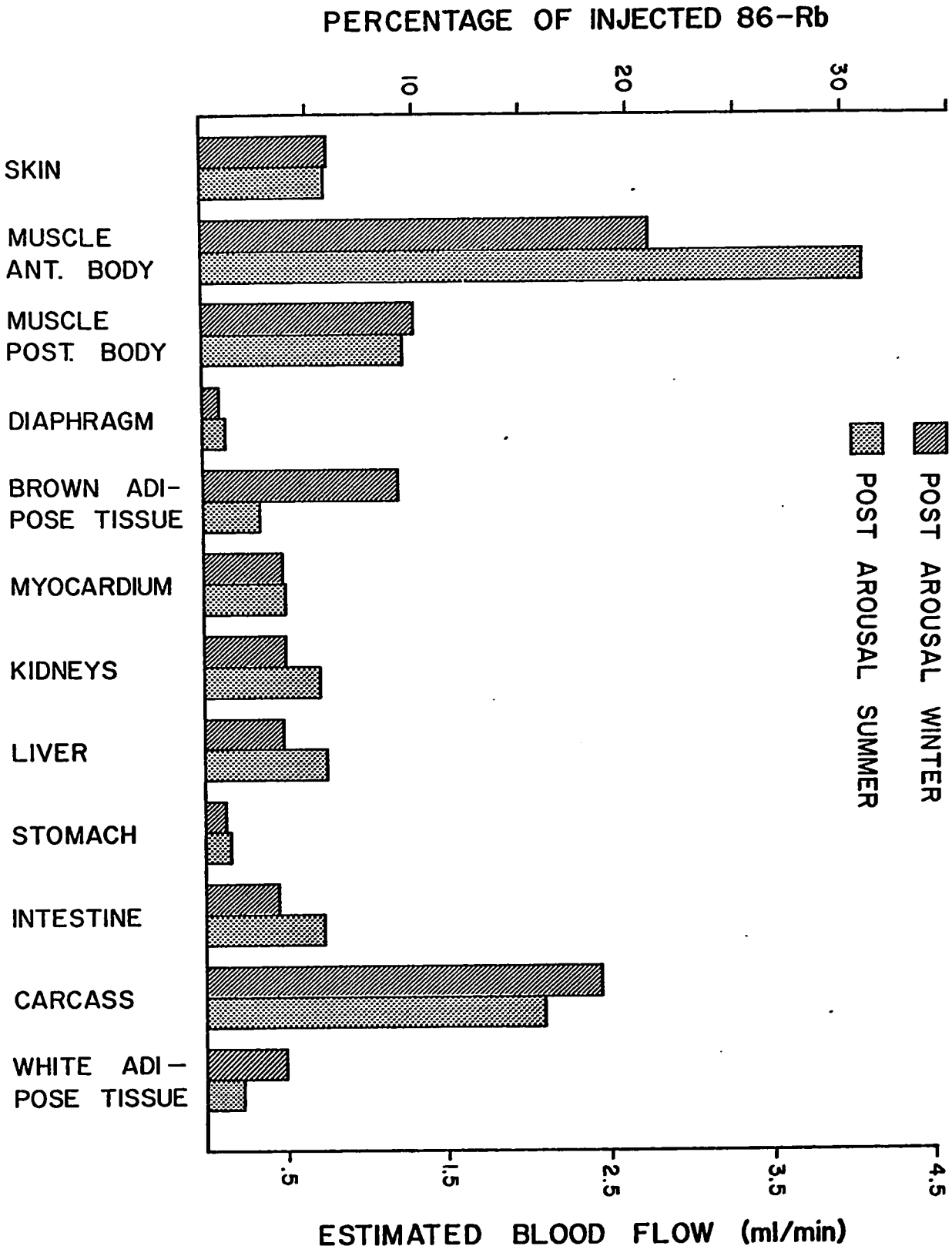

PERCENTAGE OF INJECTED 86-Rb
10
20
30
SKIN
MUSCLE ANT. BODY
MUSCLE POST. BODY
DIAPHRAGM
BROWN ADI-POSE TISSUE
MYOCARDIUM
KIDNEYS
LIVER
STOMACH
INTESTINE
CARCASS
WHITE ADI-POSE TISSUE
POST AROUSAL WINTER
POST AROUSAL SUMMER
.5
1.5
2.5
3.5
4.5
ESTIMATED BLOOD FLOW (ml/min)

Table XV. Percentage of injected 86-Rb (Rubidium) per organ or tissue of *E. fuscus*, sacrificed during post-arousal (resting) in the winter and in the summer.

	POST-AROUSAL (T_a = 22 C)			
	Winter		Summer	
Heart rate	480		480	
No. of animals	8		4	
Tissue or organ	Mean	s_d (±)	Mean	s_d (±)
Skin	6.42	0.75	5.88	0.86
Muscle ant. body	20.87	2.68	30.67	0.56
Muscle post. body	10.04	2.26	9.56	0.72
Total muscle	30.91	4.18	40.23	0.46
Diaphragm	0.86	0.24	1.10	0.11
Interscap. B.A.T.	5.09	1.35	1.52	0.88
Other B.A.T.	4.16	0.66	1.18	0.52
Total B.A.T.	9.25	1.88	2.70	1.40
Liver	3.86	0.39	5.18	1.64
Kidneys	3.96	1.60	5.54	0.80
Stomach	1.03	0.18	1.30	0.40
Intestine	3.54	0.76	5.64	0.74
Myocardium	3.68	0.40	3.82	0.71
Blood	13.95	1.20	10.12	1.61
W.A.T.	3.89	1.54	1.79	0.75
Carcass	18.66	2.17	17.15	1.57

Table XVI. Results from statistical analysis (Student-Newman-Keuls procedure) on percentages (%) of injected 86-Rb (Rubidium) per organ or tissue of *E. fuscus*, sacrificed during post-arousal (resting; T_a = 22 C) in the winter and in the summer.

Skin:	PA-W PA-S	Muscle ant. body:	PA-S PA-W	Muscle post. body:	PA-W PA-S	Total muscle:	PA-S PA-W	
Diaphragm:	PA-S PA-W	Interscap. B.A.T.:	PA-W PA-S	Other B.A.T.:	PA-W PA-S	Total B.A.T.:	PA-W PA-S	
Liver:	PA-S PA-W	Kidneys:	PA-S PA-W	Stomach:	PA-S PA-W	Intestine:	PA-S PA-W	
Myocardium:	PA-S PA-W	W.A.T.:	PA-W PA-S	Carcass:	PA-W PA-S			

PA-W: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed during post-arousal (resting) in the winter.

PA-S: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed during post-arousal (resting) in the summer.

Table XVII. Percentage of injected 86-Rb (Rubidium) per organ or tissue of *E. fuscus*, sacrificed during deep hibernation and during post-arousal (resting) in the winter.

	DEEP HIBERNATION (T_a = 5 C)		POST-AROUSAL (T_a = 22 C)	
Heart rate	12		480	
No. of animals	6		8	
Tissue or organ	Mean	s_d (±)	Mean	s_d (±)
Skin	5.70	0.55	6.42	0.75
Muscle ant. body	22.92	1.08	20.87	2.68
Muscle post. body	9.98	0.51	10.04	2.26
Total muscle	32.91	0.92	30.91	4.18
Diaphragm	0.72	0.08	0.86	0.24
Interscap. B.A.T.	2.63	0.38	5.09	1.35
Other B.A.T.	2.60	0.50	4.16	0.66
Total B.A.T.	5.23	0.85	9.25	1.88
Liver	5.13	0.56	3.86	0.39
Kidneys	1.22	0.28	3.96	1.60
Stomach	1.14	0.30	1.03	0.18
Intestine	5.15	0.79	3.54	0.76
Myocardium	2.75	0.44	3.68	0.40
Blood	15.24	1.73	13.95	1.20
W.A.T.	4.25	2.13	3.89	1.54
Carcass	20.54	1.19	18.66	2.17

Table XVIII. Results from statistical analysis (Student-Newman-Keuls procedure) on percentages (%) of injected 86-Rb (Rubidium) per organ or tissue of *E. fuscus*, sacrificed during deep hibernation (T_a = 5 C) and during post-arousal (resting; T_a = 22 C) in the winter.

Skin:	PA-W DH-W	Muscle ant. body:	DH-W PA-W	Muscle post. body:	PA-W DH-W
Total muscle:	DH-W PA-W	Diaphragm:	PA-W DH-W	Interscap. B.A.T.:	PA-W DH-W
Other B.A.T.:	PA-W DH-W	Total B.A.T.:	PA-W DH-W	Liver:	DH-W PA-W
Kidneys:	PA-W DH-W	Stomach:	DH-W PA-W	Intestine:	DH-W PA-W
Myocardium:	PA-W DH-W	W.A.T.:	DH-W PA-W	Carcass:	DH-W PA-W

DH-W: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed during deep hibernation in the winter.

PA-W: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed during post-arousal (resting) in the winter.

activities of muscle. Contrarily, in the winter, when brown fat comprises a relatively large mass, metabolic heat production by this tissue is of major importance. Such a shift in metabolic activities could explain the difference in the relative fractions of cardiac output delivered to these tissues following the arousal from hibernation.

4. Anaesthetized Bats

A comparison of the distribution of blood in anaesthetized, deeply hibernating, and post-arousal (resting) bats is presented in Figures 27 to 29. Mean values and results from statistical analysis are shown in Tables XIX to XXIV. Values for individual experiments are presented in Appendix 4, Tables 1 to 3.

Obvious differences can be seen in the distribution of blood in anaesthetized bats as compared to deeply hibernating and post-arousal (resting) bats (Fig. 27). Most prominent are higher values for skin and presumably wings (high value for carcass), and lower values for anterior muscle and brown adipose tissue of anaesthetized bats. Comparatively high percentages of cardiac output are also received by the myocardium, diaphragm and abdominal viscera. Not altered during anaesthesia is the value for posterior muscle. The only study available on the redistribution of cardiac output after Sodium pentobarbital anaesthesia, one that encompasses a variety of tissues and thus makes provision for comparison, has been performed on the monkey, *Maccaca mulatta* (Forsyth and Hoffbrand, 1970). It is used as a guide in the interpretation of present data, although variations in results due to phylogenetic differences must be expected. The need for such a comparison is explained below.

One difficulty in experimentation with heterotherms concerns the

selection of conditions under which the organism can realistically be considered as a "control" animal. During rest, immediately following activity, the average body temperature of a bat is probably similar to that of homeotherms. However, it declines as rest continues and this, in turn, is associated with other physiological changes. A steady state is probably established during rest after the body temperature has stabilized near ambient temperature. Even under this condition, the slightest disturbance causes immediate changes in heart rate, metabolic rate and body temperature (present observation). To avoid such dynamic changes during experimentation, the initial plan was to use anaesthetized bats as "control" animals. This proved to be not entirely satisfactory because anaesthesia itself was observed to produce an unexpectedly high fraction of cardiac output going to skin and low fraction to anterior muscle. Similar effects of anaesthesia on the monkey were observed by Forsyth and Hoffbrand (1970). Furthermore, other differences in the distribution of blood, but not in blood flow, between non-anaesthetized (control) and anaesthetized monkeys are comparable to those between post-arousal (resting) and anaesthetized bats. Since adult monkeys do not possess brown fat, values for this tissue are not available for comparison.

From the preceding discussion it can be assumed that the low fractions of cardiac output received by the skin and anterior muscle, respectively, are associated with Sodium pentobarbital anaesthesia and that anaesthetized bats cannot serve as "control" animals. The physiological state existing approximately one hour following arousal from hibernation shows a pattern in the distribution of blood which

closely resembles that reported for non-anaesthetized (control) monkeys. In bats, this pattern probably undergoes some changes as rest continues and the body temperature declines. Therefore, the term "control" animal has not been used in this study but instead prevailing physiological conditions of the organism are described whenever comparisons are made. Nevertheless, worthwhile information is obtained from Sodium pentobarbital induced circulatory changes in bats and this can be discussed accordingly.

All organs and tissues except skeletal muscle and brown fat receive comparatively high fractions of cardiac output in anaesthetized bats (Fig. 27; Table XIX). This could mean that blood vessels, other than those of skeletal muscle and brown fat, have reduced vasomotor tone following the administration of Sodium pentobarbital. Therefore, the lower values for skin during deep hibernation (Tables XIX to XX) and the lack of significant differences between the percentages of cardiac output delivered to this tissue in deeply hibernating and post-arousal (resting) bats (Table XX) are taken as evidence of a relatively high vasomotor tone in this tissue during deep hibernation in the winter (Figs. 27 and 28). There appears to be less vasomotor tone during induced hibernation in the summer (Fig. 28, Tables XXI and XXII). The similarity in the fraction of cardiac output delivered to the carcass of anaesthetized and hibernating bats in summer (Fig. 28) suggests decreased vasomotor tone in the blood vessels supplying the wings. Because the surface area of wings is large, cooling of the circulating blood may be considerable in bats subjected to cold during the summer. The comparatively high fraction of cardiac output reaching the myocardium of anaesthetized bats (Fig. 27) is

Fig. 27. Distribution of blood in lightly anaesthetized (HR = 340 beats/min; T_a = 22 C) *E. fuscus* in the summer, in deeply hibernating (HR = 12 beats/min; T_a = 5 C) *E. fuscus* in the winter, and in post-arousal (resting; HR = 480 beats/min; T_a = 22 C) *E. fuscus* in the winter. Percentage of injected 86-Rb per organ or tissue represents percentage of cardiac output received by that organ or tissue (Sapirstein, 1958). Mean values, standard deviations and number of measurements are presented in Table XIX.

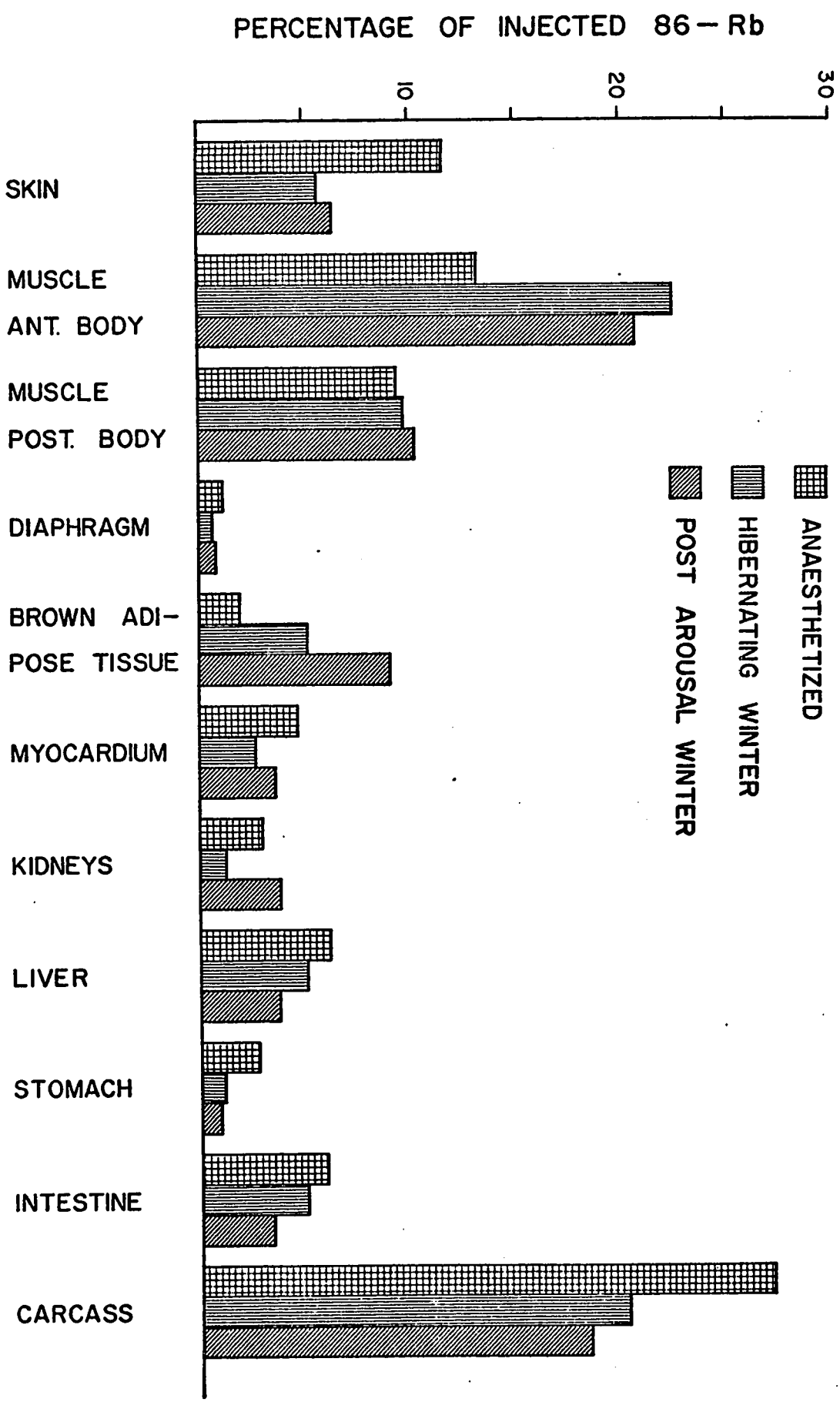

PERCENTAGE OF INJECTED 86 — Rb
10
20
30
SKIN
MUSCLE
ANT. BODY
MUSCLE
POST. BODY
DIAPHRAGM
BROWN ADI-
POSE TISSUE
MYOCARDIUM
KIDNEYS
LIVER
STOMACH
INTESTINE
CARCASS
ANAESTHETIZED
HIBERNATING WINTER
POST AROUSAL WINTER

Table XX. Results from statistical analysis (Student-Newman-Keuls procedure) on percentages (%) of injected 86-Rb (Rubidium) per organ or tissue of *E. fuscus*, sacrificed during light anaesthesia (non-hibernating; T_a = 22 C) in the summer, during deep hibernation (T_a = 5 C) and during post-arousal (resting; T_a = 22 C) in the winter.

Skin:	A-NH PA-W DH-W	Muscle ant. body:	DH-W PA-W A-NH	Muscle post. body:	PA-W DH-W A-NH
Total muscle:	DH-W PA-W A-NH	Diaphragm:	A-NH PA-W DH-W	Interscap. B.A.T.:	PA-W DH-W A-NH
Other B.A.T.:	PA-W DH-W A-NH	Total B.A.T.:	PA-W DH-W A-NH	Liver:	A-NH DH-W PA-W
Kidneys:	PA-W A-NH DH-W	Stomach:	A-NH DH-W PA-W	Intestine:	A-NH DH-W PA-W
Myocardium:	A-NH PA-W DH-W	W.A.T.:	DH-W PA-W A-NH	Carcass:	A-NH DH-W PA-W

A-NH: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed in a lightly anaesthetized, non-hibernating state during the summer.

DH-W: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed during deep hibernation in the winter.

PA-W: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed during post-arousal (resting) in the winter.

similar to that for the monkey (Forsyth and Hoffbrand, 1970) and for the dog (Essex *et al.*, 1940). This fraction is significantly lower during hibernation in the winter but not during hibernation in the summer (Fig. 28; Tables XXI and XXII). This suggests that the coronary blood vessels of the bats subjected to cold in the summer are greatly dilated. Fractions of cardiac output delivered to the kidneys are significantly different between anaesthetized bats and those hibernating in the winter (Fig. 28; Tables XXI and XXII) but not between anaesthetized bats and those hibernating in the summer (Fig. 28; Tables XXI and XXII). This is in contrast to the results between bats hibernating in the summer and winter (Fig. 28; Table XXII) and implies comparatively low vasomotor tone in renal blood vessels in the former group of bats.

The differences in the distribution of blood in the two groups of post-arousal (resting) bats (Fig. 26), and between anaesthetized and post-arousal (resting) bats in the winter (Fig. 28), have been discussed above. Noteworthy is that the fractional delivery in cardiac output to liver and intestine is significantly higher at the 5 percent level of probability in anaesthetized as compared to post-arousal (resting) bats in the winter, but not between anaesthetized and post-arousal (resting) bats in the summer.

The mechanisms involved in cardiovascular changes following the administration of Sodium pentobarbital are probably complex and not fully understood (Forsyth and Hoffbrand, 1970). Nevertheless, this drug produces reduced vascular tone in the blood vessels of a variety of organs and, although the extent to which blood vessels dilate is only speculation, the comparisons made in this study provide new information on circulatory adjustments during deep hibernation in the winter.

Fig. 28. Distribution of blood in lightly anaesthetized (HR = 340 beats/min; T_a = 22 C) *E. fuscus* in the summer, and in deeply hibernating (HR = 12 beats/min; T_a = 5 C) *E. fuscus* in the summer and in the winter. Percentage of injected 86-Rb (Rubidium) per organ or tissue represents percentage of cardiac output received by that organ or tissue (Sapirstein, 1958). Mean values, standard deviations and number of measurements are presented in Table XXI.

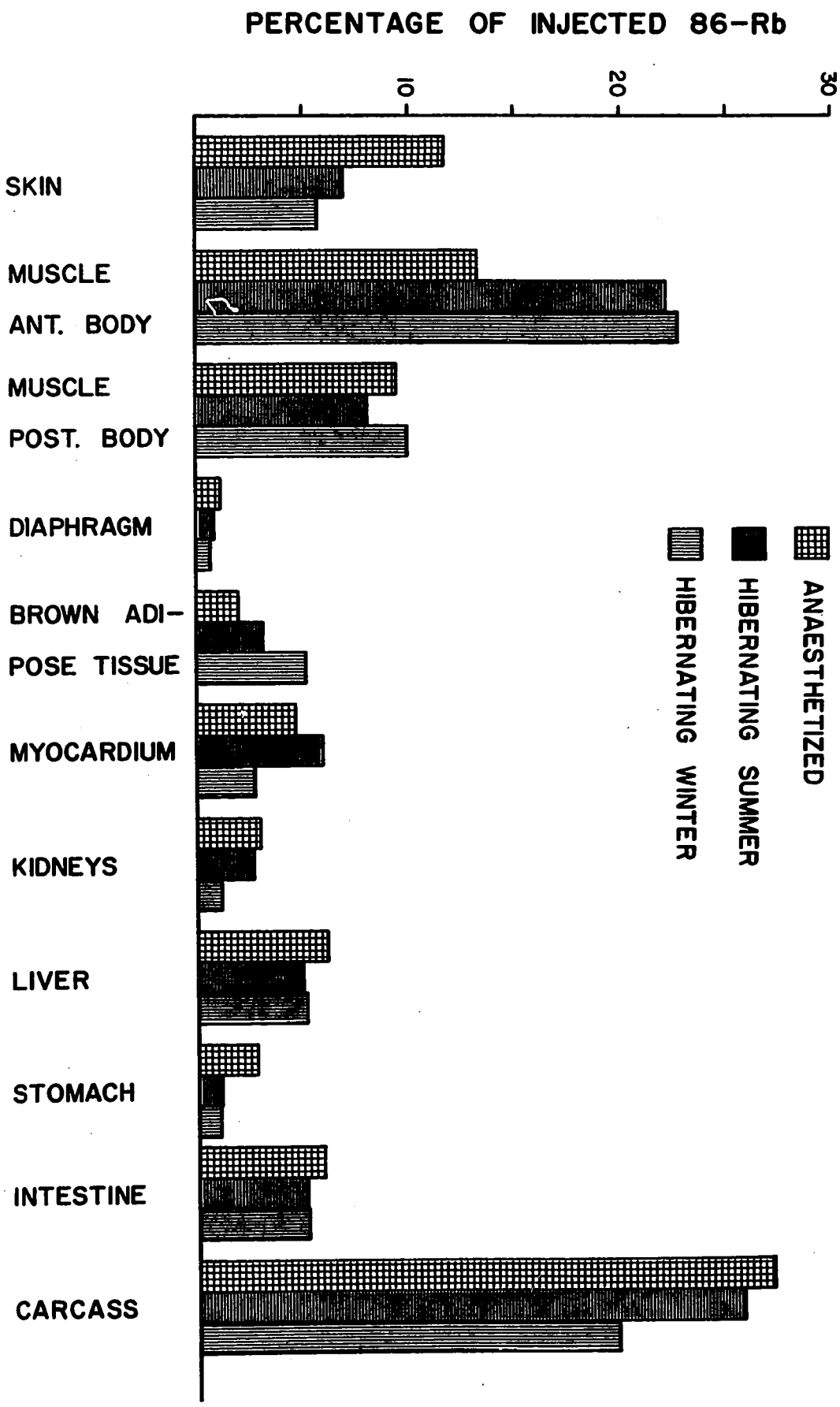

PERCENTAGE OF INJECTED 86-Rb
10
20
30
SKIN
MUSCLE
ANT. BODY
MUSCLE
POST. BODY
DIAPHRAGM
BROWN ADI-
POSE TISSUE
MYOCARDIUM
KIDNEYS
LIVER
STOMACH
INTESTINE
CARCASS
ANAESTHETIZED
HIBERNATING SUMMER
HIBERNATING WINTER

Table XXI. Percentage of injected 86-Rb (Rubidium) per organ or tissue of *E. fuscus*, sacrificed during light anaesthesia (non-hibernating) in the summer, and during deep hibernation in the summer and in the winter.

	ANAESTHESIA (NON-HIBERNATING) Summer (T_a = 22 C)		DEEP HIBERNATION Summer (T_a = 5 C)		DEEP HIBERNATION Winter (T_a = 5 C)	
Heart rate	340		12		12	
No. of animals	10		5		6	
Tissue or organ	Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)
Skin	11.68	2.32	6.98	0.70	5.70	0.55
Muscle ant. body	13.37	3.00	22.24	3.65	22.92	1.08
Muscle post. body	9.47	1.57	8.11	1.30	9.98	0.51
Total muscle	22.83	3.57	30.35	4.78	32.91	0.92
Diaphragm	1.09	0.20	0.91	0.07	0.72	0.08
Interscap. B.A.T.	1.00	0.82	1.65	0.47	2.63	0.38
Other B.A.T.	0.99	0.51	1.57	0.38	2.60	0.50
Total B.A.T.	1.99	1.33	3.22	0.84	5.23	0.85
Liver	6.21	1.13	5.00	1.01	5.13	0.56
Kidneys	3.00	1.16	2.74	0.84	1.22	0.28
Stomach	2.91	0.37	1.20	0.20	1.14	0.30
Intestine	6.07	1.30	5.21	1.61	5.15	0.79
Myocardium	4.71	1.39	5.85	0.63	2.75	0.44
Blood	10.58	1.55	11.41	1.81	15.24	1.73
W.A.T.	1.56	0.72	1.08	0.62	4.25	2.13
Carcass	27.46	2.90	26.05	0.89	20.54	1.19

Table XXII. Results from statistical analysis (Student-Newman-Keuls procedure) on percentages (%) of injected 86-Rb (Rubidium) per organ or tissue of *E. fuscus*, sacrificed during light anaesthesia (non-hibernating; T_a = 22 C) and during deep hibernation (T_a = 5 C) in the summer and in the winter.

Skin:	A-NH DH-S DH-W	Muscle ant. body:	DH-W DH-S A-NH	Muscle post. body:	DH-W A-NH DH-S
Total muscle:	DH-W DH-S A-NH	Diaphragm:	A-NH DH-S DH-W	Interscap. B.A.T.:	DH-W DH-S A-NH
Other B.A.T.:	DH-W DH-S A-NH	Total B.A.T.:	DH-W DH-S A-NH	Liver:	A-NH DH-W DH-S
Kidneys:	A-NH DH-S DH-W	Stomach:	A-NH DH-S DH-W	Intestine:	A-NH DH-S DH-W
Myocardium:	DH-S A-NH DH-W	W.A.T.:	DH-W A-NH DH-S	Carcass:	A-NH DH-S DH-W

A-NH: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed in a lightly anaesthetized, non-hibernating state during the summer.

DH-S: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed during deep hibernation in the summer.

DH-W: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed during deep hibernation in the winter.

Fig. 29. Distribution of blood in lightly anaesthetized (HR = 340 beats/min; T_a = 22 C) *E. fuscus* in the summer, and in post-arousal (resting; HR = 480 beats/min) *E. fuscus* in the summer and in the winter. Percentage of injected 86-Rb (Rubidium) per organ or tissue represents percentage of cardiac output received by that organ or tissue (Sapirstein, 1958). Mean values, standard deviations and number of measurements are presented in Table XXIII.

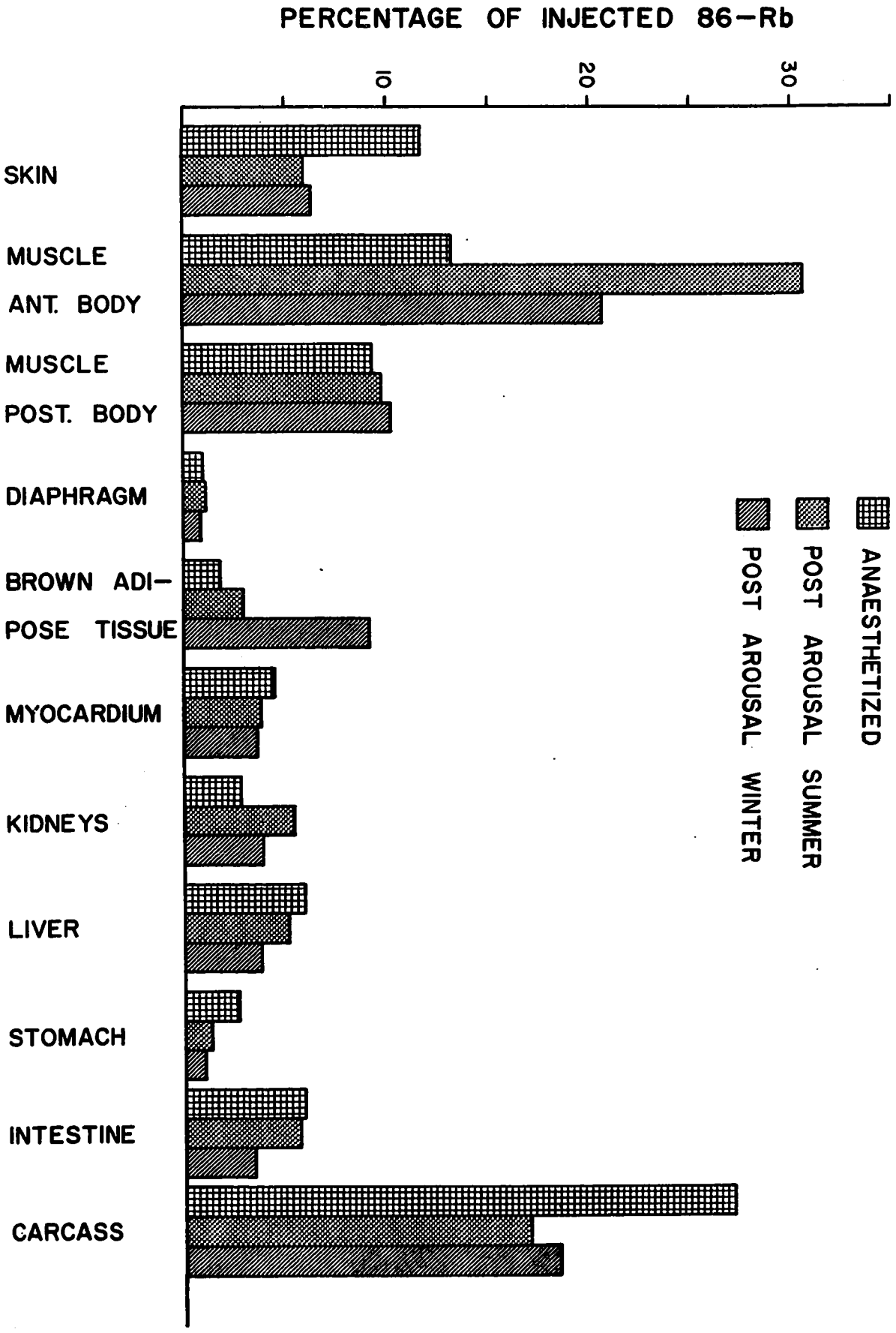

PERCENTAGE OF INJECTED 86-Rb
10
20
30
SKIN
MUSCLE
ANT. BODY
MUSCLE
POST. BODY
DIAPHRAGM
BROWN ADI-
POSE TISSUE
MYOCARDIUM
KIDNEYS
LIVER
STOMACH
INTESTINE
CARCASS
ANAESTHETIZED
POST AROUSAL SUMMER
POST AROUSAL WINTER

Table XXIII. Percentage of injected 86-Rb (Rubidium) per organ or tissue of *E. fuscus*, sacrificed during light anaesthesia (non-hibernating) in the summer, and during post-arousal (resting) in the summer and in the winter.

	ANAESTHESIA (NON-HIBERNATING) Summer (T_a = 22 C)		POST-AROUSAL (RESTING) Summer (T_a = 22 C)		POST-AROUSAL (RESTING) Winter (T_a = 22 C)	
Heart rate	340		480		480	
No. of animals	10		4		8	
Tissue or organ	Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)
Skin	11.68	2.32	5.88	0.86	6.42	0.75
Muscle ant. body	13.37	3.00	30.67	0.56	20.87	2.68
Muscle post. body	9.47	1.57	9.56	0.72	10.04	2.26
Total muscle	22.83	3.57	40.23	0.46	30.91	4.18
Diaphragm	1.09	0.20	1.10	0.11	0.86	0.24
Interscap. B.A.T.	1.00	0.82	1.52	0.88	5.09	1.35
Other B.A.T.	0.99	0.51	1.18	0.52	4.16	0.66
Total B.A.T.	1.99	1.33	2.70	1.40	9.25	1.88
Liver	6.21	1.13	5.18	1.64	3.86	0.39
Kidneys	3.00	1.16	5.54	0.80	3.96	1.60
Stomach	2.91	0.37	1.30	0.40	1.03	0.18
Intestine	6.07	1.30	5.64	0.74	3.54	0.76
Myocardium	4.71	1.39	3.82	0.71	3.68	0.40
Blood	10.58	1.55	10.12	1.61	13.95	1.20
W.A.T.	1.56	0.72	1.79	0.75	3.89	1.54
Carcass	27.46	2.90	17.15	1.57	18.66	2.17

Table XXIV. Results from statistical analysis (Student-Newman-Keuls procedure) on percentages (%) of injected 86-Rb (Rubidium) per organ or tissue of *E. fuscus*, sacrificed during light anaesthesia (non-hibernating; T_a = 22 C) and during post-arousal (resting; T_a = 22 C) in the summer and in the winter.

Skin:	A-NH PA-W PA-S	Muscle ant. body:	PA-S PA-W A-NH	Muscle post. body:	PA-W PA-S A-NH
Total muscle:	PA-S PA-W A-NH	Diaphragm:	PA-S A-NH PA-W	Interscap. B.A.T.:	PA-W PA-S A-NH
Other B.A.T.:	PA-W PA-S A-NH	Total B.A.T.:	PA-W PA-S A-NH	Liver:	A-NH PA-S PA-W
Kidneys:	PA-S PA-W A-NH	Stomach:	A-NH PA-S PA-W	Intestine:	A-NH PA-S PA-W
Myocardium:	A-NH PA-S PA-W	W.A.T.:	PA-W PA-S A-NH	Carcass:	A-NH PA-S PA-W

A-NH: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed in a lightly anaesthetized, non-hibernating state during the summer.

PA-S: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed during post-arousal (resting) in the summer.

PA-W: refers to the mean percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed during post-arousal (resting) in the winter.

ESTIMATED BLOOD FLOW

Cardiac output was estimated by multiplying heart rate (beats/min) by 0.024 ml (Section: Materials and Methods). Knowing the fractions of cardiac output (percentages of injected 86-Rb) delivered to various organs during similar physiological conditions, capillary blood flow could be calculated as indicated (Section: Materials and Methods). As mean values were used to estimate the percentage uptake of 86-Rb or the fraction of cardiac output received by given organs during particular physiological states, statistical analysis for nutritional organ blood flow could not be performed. Calculating blood flow values for all organs of each individual bat used in the experiment would have little meaning since accurate analysis was done for the study on distribution of blood and because the values for blood flow are an estimation inasmuch as cardiac output has not been measured directly.

Capillary blood flow in various organs of *E. fuscus* was estimated during deep hibernation (Fig. 21), arousal from hibernation (Figs. 30 to 33), and about one hour following the arousal process (Fig. 26) in the summer and in the winter. Capillary blood flow, as compared among anaesthetized, hibernating, and post-arousal (resting) bats, is illustrated in Figures 34 to 36. Calculated mean values are presented in Tables XXV and XXVI. Because the average heart rate (12 beats/min) is similar in bats hibernating in the summer and in the winter, the resulting cardiac outputs of the two groups are assumed to be the same. Consequently, a single illustration (Fig. 21) presents the percentage organ uptake of injected 86-Rb (fraction of cardiac output) and estimated nutritional organ blood flow. Likewise for bats in a post-arousal

(resting) condition in the summer and in the winter, the cardiac outputs are assumed to be the same (heart rate = 480 beats/min) and a single illustration (Fig. 26) shows the percentage organ uptake of injected 86-Rb and estimated nutritional blood flow.

Blood flow to all organs and tissues is greatly reduced in deep hibernation as compared to the post-arousal (resting) state (Figs. 21, 26, and 34). That this reduction is a consequence of a considerably diminished cardiac output can be deduced from the estimated cardiac output values (Tables XXV to XXVI). As is the case with the fractional delivery of cardiac output, blood flow to most organs and tissues of deeply hibernating bats in the winter (Fig. 21) is approximately proportional to the percentage weights of these organs and tissues (Table V). The most important exceptions to this generalization pertain to the myocardium, skin, and white fat. On a percentage weight basis, the myocardium receives approximately three times as great a flow as most other tissues, but the skin and presumably the wings (low value for carcass) receive only about one-half as much. Relative blood flow is lowest for white adipose tissue.

Blood flow to the myocardium, kidneys, skin and presumably wings (increased value for carcass) is considerably higher in bats subjected to cold in the summer as compared to those hibernating in the winter. While these are actual differences, the lower blood flow to brown adipose tissue in the former group of bats is a direct function of their proportionally lower brown fat mass. The relevance of these findings in relation to hibernation as a seasonal phenomenon has been mentioned earlier and will be discussed more fully in a subsequent section.

With the initiation of arousal from hibernation in winter, there is an increase in nutritional blood flow to a number of organs and tissues (Table XXV; Figs. 30 and 31), but the extent to which capillary flow is augmented varies considerably among different organs. The highest flow rate increment during early arousal is that for brown adipose tissue (Table XXV). As early as six minutes after initial arousal, at a heart rate approximating 40 beats per minute, capillary flow in this tissue shows a sixfold increment over its corresponding value in deep hibernation. By this time, anterior muscle, diaphragm, and myocardium receive five-, four- and threefold increments, respectively. A threefold augmentation is noticed also for posterior muscle, but capillary flow in the abdominal viscera shows little or no change at this time. Thus, even during early arousal, there is a marked gradation in flow rate increments between most organs of the anterior and posterior body. As arousal proceeds, capillary flow rate increases in all organs although the fraction of cardiac output delivered to abdominal viscera, skin and posterior muscle continues to decline (Figs. 22, 23; Table XIII). This condition is readily understandable inasmuch as the two phenomena, that is, progressively increasing and simultaneously shifting cardiac output, are coordinated such that the magnitude of flow rate increments differs for different organs. Consequently, flow rates in various organs and tissues reach their maxima at different times during arousal. The greatest capillary flow rate increment in brown adipose tissue occurs between heart rates of 40 to 80 beats per minute and its maximum blood flow is established at a heart rate of 480 beats per minute. None of the other tissues and organs, including the heart, obtain maximum capillary

flow prior to peak arousal. Skin, kidneys, stomach, and intestine attain their highest blood flow values under post-arousal conditions after capillary flow in skeletal muscle and brown fat has declined by considerable amounts.

From the above it appears that with the progressive increase in cardiac output during early arousal there is a progressive decrease in vascular tone of the vessels to brown adipose tissue, anterior muscle and diaphragm. This causes a non-proportional increase in blood flow such that a relatively high fraction of the cardiac output is delivered to the organs of the anterior body and a relatively small fraction supplies the abdominal viscera. Capillary flow in brown adipose tissue differs in that the greatest flow rate increments and maximum flow occur earlier in arousal than do similar events in other tissues and organs. Inasmuch as there exists a relationship between aerobic metabolism and nutritional blood flow (Honig, 1968) and hence metabolic heat production, the present finding corroborates other data which imply that brown adipose tissue is a major source of heat during the arousal from hibernation (Smith and Hock, 1963; Hayward and Lyman, 1967). Probably of greatest importance is the fact that the brown fat temperature increases more rapidly at an earlier time in arousal (Section: Body Temperature) than do temperatures of other tissues. As a result, heat will be transferred from this to other tissues and organs. As their temperature rises, metabolic rate and consequently nutritional blood flow in these tissues and organs will also be enhanced.

In late arousal there is a reversal of the events that take place during early arousal. As blood flow through brown adipose tissue declines

Fig. 30. Sequential changes in capillary blood flow to various organs and tissues of *E. fuscus* during the arousal from hibernation (T_a = 5 C) in the winter. The study is based on the regional distribution of blood as measured by the 86-Rb (Rubidium) method (Sapirstein, 1958) at various heart rates (Table XIII) during arousal. Flow rate values (Table XXV) are approximations inasmuch as a constant theoretical stroke volume of 0.024 ml has been assumed (Section: Materials and Methods).

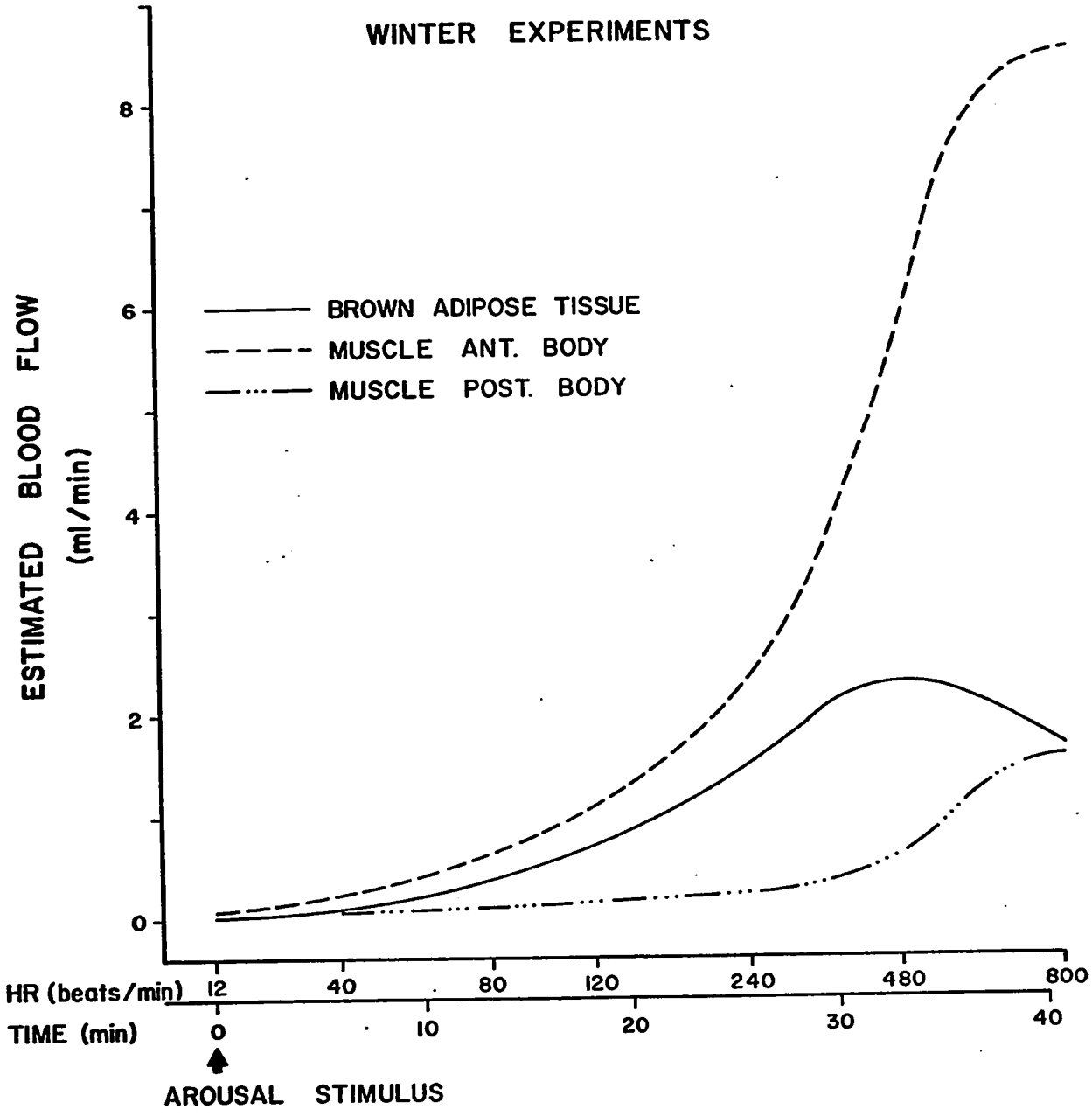

WINTER EXPERIMENTS
ESTIMATED BLOOD FLOW (ml/min)
8
6
4
2
0
BROWN ADIPOSE TISSUE
MUSCLE ANT. BODY
MUSCLE POST. BODY
HR (beats/min) 12 40 80 120 240 480 800
TIME (min) 0 10 20 30 40
AROUSAL STIMULUS

Fig. 31. Sequential changes in capillary blood flow to various organs and tissues of *E. fuscus* during the arousal from hibernation (T_a = 5 C) in the winter. The study is based on the regional distribution of blood as measured by the 86-Rb (Rubidium) method (Sapirstein, 1958) at various heart rates (Table XIII) during arousal. Flow rate values (Table XXV) are approximations inasmuch as a constant theoretical stroke volume of 0.024 ml has been assumed (Section: Materials and Methods).

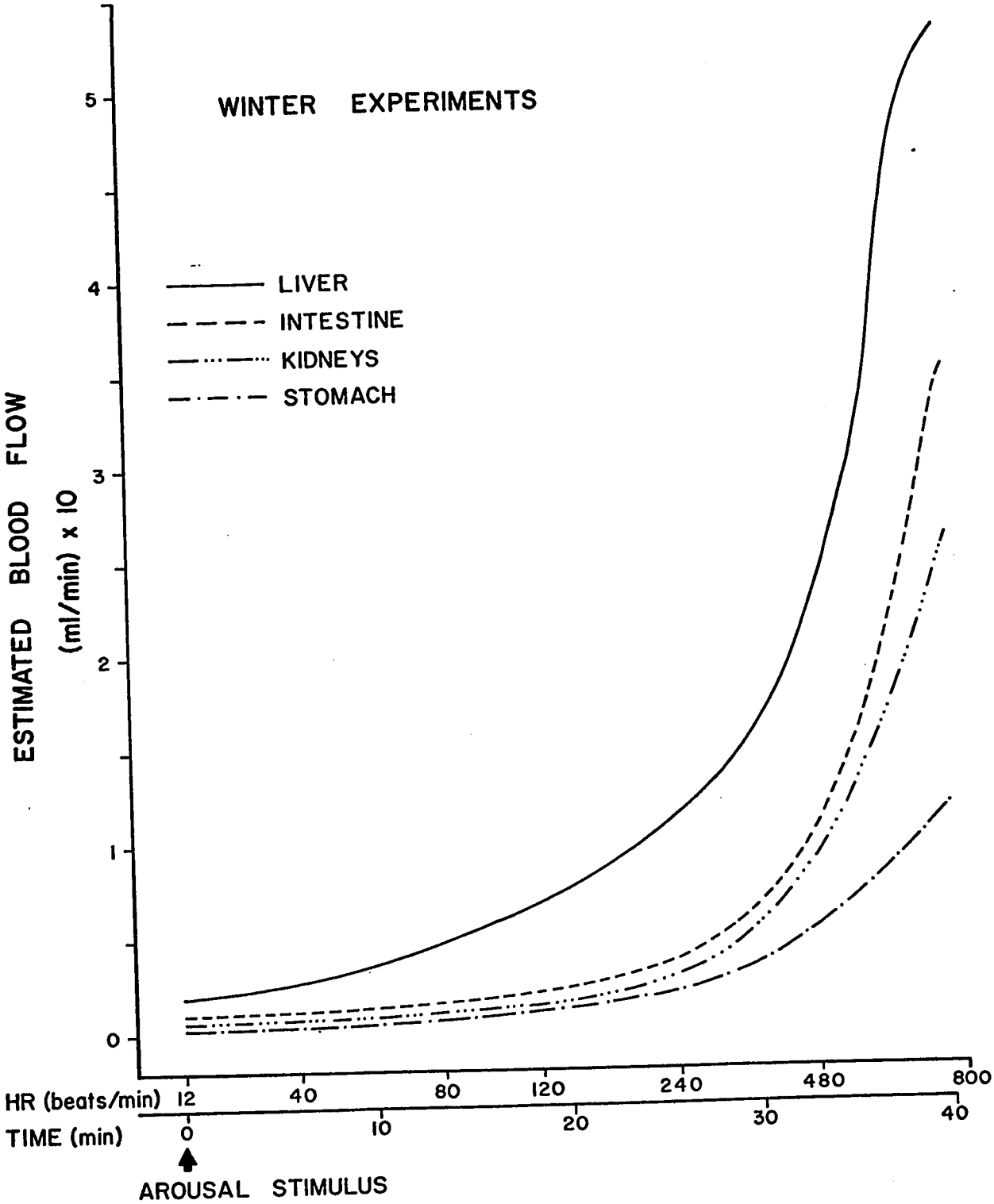

WINTER EXPERIMENTS
LIVER
INTESTINE
KIDNEYS
STOMACH
ESTIMATED BLOOD FLOW
(ml/min) x 10
5
4
3
2
1
0
HR (beats/min) 12 40 80 120 240 480 800
TIME (min) 0 10 20 30 40
AROUSAL STIMULUS

Table XXV. Estimated capillary blood flow (ml/min) in various organs and heart rates (HR) during the arousal from hibernation, and

	DEEP HIBERNATION (T_a = 5 C)	AROUSAL FROM HIBERNATION			
HR	12	40	80	120	180
Skin	0.019	0.037	0.062	0.080	0.152
Muscle ant. body	0.078	0.392	0.668	1.161	1.633
Muscle post. body	0.034	0.109	0.163	0.221	0.229
Total muscle	0.112	0.501	0.831	1.382	1.862
Diaphragm	0.002	0.008	0.016	0.024	0.038
Interscap. B.A.T.	0.009	0.062	0.281	0.339	0.580
Other B.A.T.	0.009	0.056	0.199	0.304	0.454
Total B.A.T.	0.018	0.118	0.480	0.643	1.034
Liver	0.017	0.027	0.048	0.069	0.067
Kidneys	0.004	0.006	0.014	0.015	0.020
Stomach	0.004	0.005	0.007	0.009	0.015
Intestine	0.018	0.011	0.020	0.017	0.026
Myocardium	0.009	0.027	0.064	0.111	0.224
W.A.T.	0.014	0.022	0.041	0.054	0.077
Carcass	0.070	0.196	0.334	0.475	0.805
Estimated cardiac output (ml/min)	0.290	0.960	1.920	2.880	4.320

Blood flow values were calculated according to the formula:

1. Cardiac Output (CO) = Stroke Volume (SV) x Heart

2. Organ capillary blood flow (ml/min) = CO (ml/min)

A constant, estimated stroke volume of 0.024 ml was assumed.

tissues of *E. fuscus*, sacrificed during deep hibernation, at different during post-arousal (resting) in the winter.

(T_a = 5 C) IN THE WINTER						POST-AROUSAL (T_a = 22 C)
240	300	360	480	600	800	480
0.166	0.215	0.279	0.346	0.679	0.712	0.859
2.287	2.749	3.635	4.954	6.407	8.464	2.794
0.266	0.412	0.424	0.393	0.723	1.548	1.344
2.553	3.161	4.059	5.347	7.130	10.012	4.138
0.054	0.071	0.095	0.130	0.138	0.206	0.115
0.903	0.913	0.936	1.282	1.180	1.074	0.681
0.683	0.785	0.764	1.061	0.946	0.949	0.557
1.586	1.698	1.700	2.343	2.126	2.023	1.238
0.083	0.131	0.159	0.240	0.316	0.532	0.517
0.032	0.042	0.042	0.093	0.068	0.260	0.530
0.018	0.025	0.034	0.050	0.062	0.116	0.137
0.034	0.041	0.062	0.111	0.096	0.350	0.474
0.272	0.406	0.483	0.772	0.794	1.022	0.493
0.099	0.153	0.134	0.151	0.290	0.477	0.521
0.864	1.254	1.592	1.937	2.702	3.491	2.498
5.760	7.200	8.640	11.520	14.400	19.200	11.520

Rate (HR).

$$\times \frac{\text{Organ activity (counts/min)}}{\text{Total injected activity (counts/min) - Activity of blood (counts/min)}}.$$

there is a sharp rise of capillary flow in the myocardium, then in the liver, skin, and posterior muscle. Subsequently, when flow rate increments to anterior muscle become less, increasingly larger amounts of blood are directed to the abdominal viscera. This shift apparently continues until after arousal when, with the animal at rest, the distribution of cardiac output is nearly comparable to that in deep hibernation (Tables XVII and XVIII). Thus the major modification in blood flow between hibernating and post-arousal (resting) bats involves differences in cardiac output rather than alterations in its distribution.

The relative differences in capillary blood flow between bats arousing in the winter (Figs. 30 to 31; Table XXV) and summer (Figs. 32 to 33; Table XXVI) are essentially those that have been discussed for the distribution of blood in the two groups of bats. In the summer, capillary blood flow in all organs and tissues increases following initial arousal, that is, between heart rates of 12 to 40 beats per minute. However, the relative increments during this interval are not the same in summer and winter experiments. Capillary blood flow to the skin, myocardium, and the abdominal viscera is definitely higher and that to brown adipose tissue is considerably lower in bats arousing during the summer. The reduced blood flow to brown adipose tissue of bats used in summer experiments is approximately proportional to the lower percentage lean body weight of this tissue of bats during the summer season (Table V). From the statistical analysis on the distribution of blood (App. 6; Table 5), it can be concluded that blood flow to the myocardium, kidneys and intestine is significantly higher only during the first half of the arousal process (HR = 180 to 360 beats/min) in bats studied during the summer. During

Fig. 32. Sequential changes in capillary blood flow to various organs and tissues of *E. fuscus* during the arousal from hibernation (T_a = 5 C) in the summer. The study is based on the regional distribution of blood as measured by the 86-Rb (Rubidium) method (Sapirstein, 1958) at various heart rates (Table XIV) during arousal. Flow rate values (Table XXVI) are approximations inasmuch as a constant theoretical stroke volume of 0.024 ml has been assumed (Section: Materials and Methods).

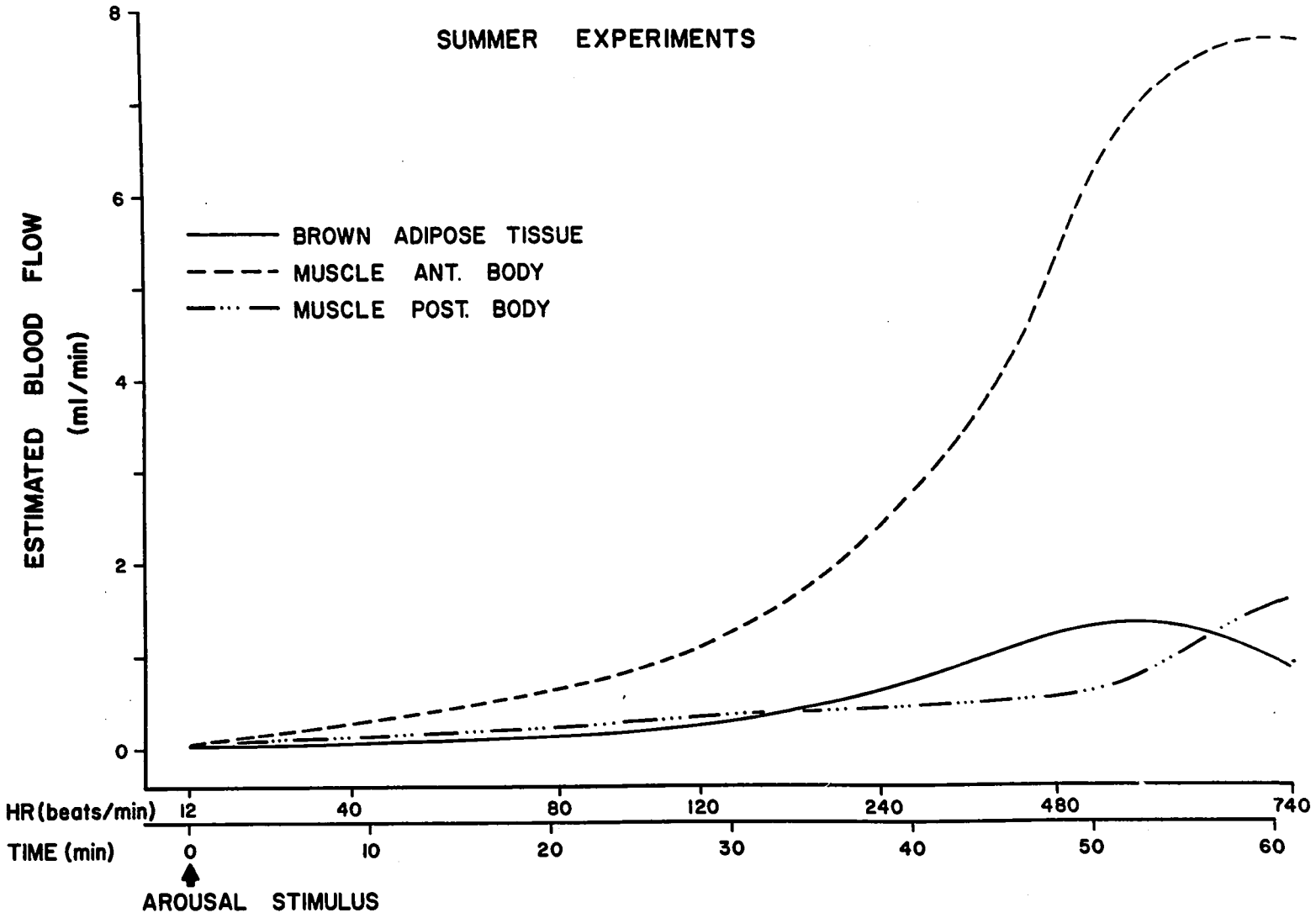

SUMMER EXPERIMENTS
ESTIMATED BLOOD FLOW (ml/min)
BROWN ADIPOSE TISSUE
MUSCLE ANT. BODY
MUSCLE POST. BODY
8
6
4
2
0
HR (beats/min)
12
40
80
120
240
480
740
TIME (min)
0
10
20
30
40
50
60
AROUSAL STIMULUS

Fig. 33. Sequential changes in capillary blood flow to various organs and tissues of *E. fuscus* during the arousal from hibernation (T_a = 5 C) in the summer. The study is based on the regional distribution of blood as measured by the 86-Rb (Rubidium) method (Sapirstein, 1958) at various heart rates (Table XIV) during arousal. Flow rate values (Table XXVI) are approximations inasmuch as a constant theoretical stroke volume of 0.024 ml has been assumed (Section: Materials and Methods).

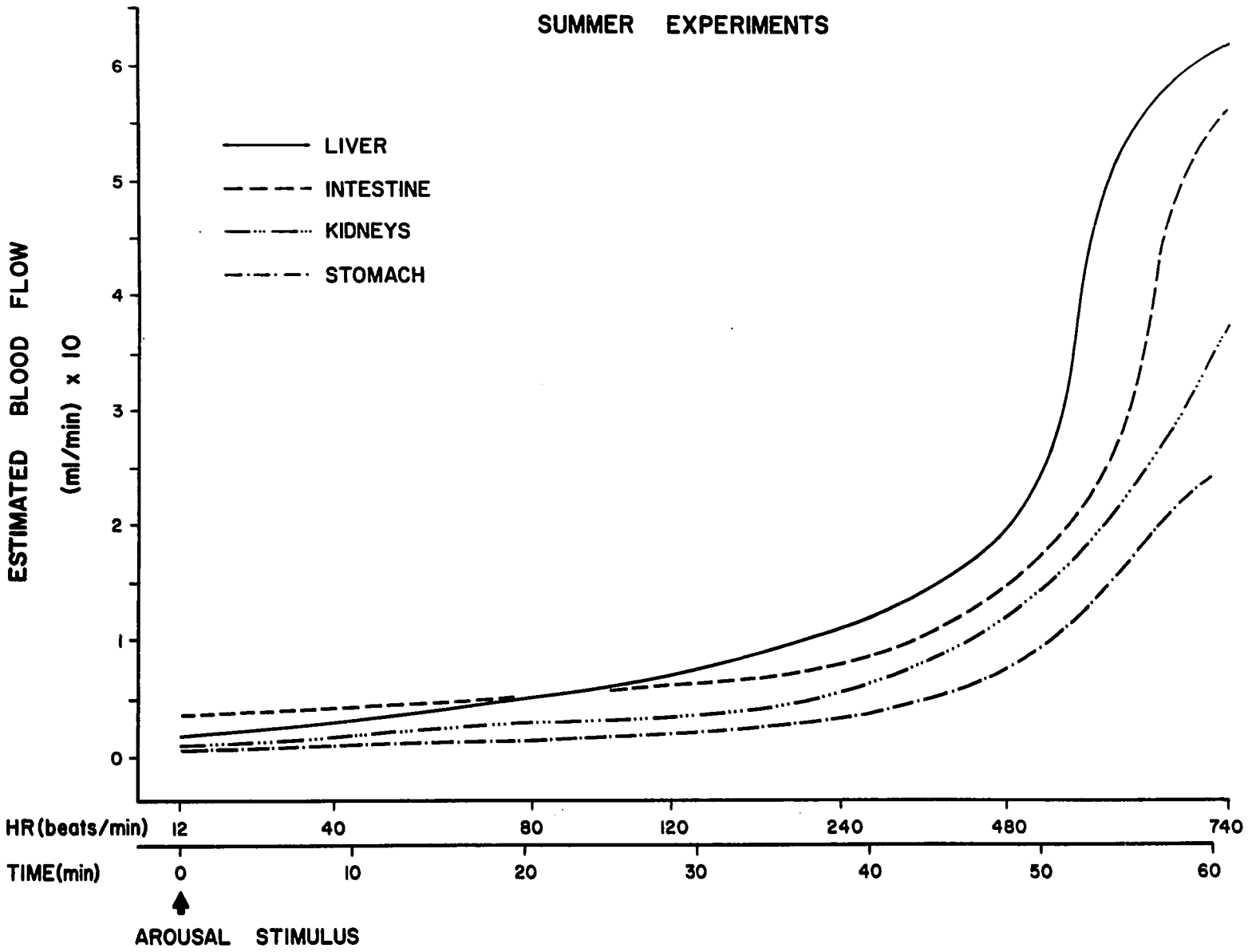

SUMMER EXPERIMENTS
LIVER
INTESTINE
KIDNEYS
STOMACH
ESTIMATED BLOOD FLOW
(ml/min) x 10
0
1
2
3
4
5
6
HR(beats/min)
12
40
80
120
240
480
740
TIME(min)
0
10
20
30
40
50
60
AROUSAL STIMULUS

Table XXVI. Estimated capillary blood flow (ml/min) in various organs and heart rates (HR) during the arousal from hibernation, during state in the summer.

	DEEP HIBERNATION (T_a = 5 C)	AROUSAL FROM HIBERNATION			
HR	12	40	80	120	180
Skin	0.030	0.060	0.133	0.213	0.243
Muscle ant. body	0.073	0.311	0.740	1.025	1.802
Muscle post. body	0.026	0.113	0.245	0.219	0.488
Total muscle	0.099	0.424	0.985	1.244	2.290
Diaphragm	0.003	0.013	0.020	0.031	0.044
Interscap. B.A.T.	0.005	0.037	0.051	0.171	0.196
Other B.A.T.	0.005	0.024	0.043	0.147	0.186
Total B.A.T.	0.010	0.061	0.094	0.318	0.382
Liver	0.016	0.035	0.053	0.112	0.064
Kidneys	0.009	0.017	0.023	0.029	0.042
Stomach	0.004	0.011	0.024	0.022	0.022
Intestine	0.017	0.048	0.048	0.038	0.036
Myocardium	0.019	0.038	0.073	0.178	0.184
W.A.T.	0.004	0.008	0.025	0.029	0.040
Carcass	0.085	0.242	0.441	0.665	0.970
Estimated cardiac output (ml/min)	0.290	0.960	1.920	2.880	4.320

Blood flow values were calculated according to the formula:

1. Cardiac Output (CO) = Stroke Volume (SV) x Heart
2. Organ capillary blood flow (ml/min) = CO (ml/min)

A constant, estimated stroke volume of 0.024 ml was assumed.

tissues of *E. fuscus*, sacrificed during deep hibernation, at different post-arousal (resting), and in a lightly anaesthetized, non-hibernating

(T_a = 5 C) IN THE SUMMER					POST-AROUSAL (T_a = 22 C)	NON-HIBERNATING (T_a = 22 C)
240	360	480	600	740	480	340
0.347	0.659	0.862	0.864	0.981	0.754	1.065
2.459	3.725	5.051	6.628	7.713	3.931	1.220
0.487	0.565	0.623	0.602	1.619	1.225	0.864
2.946	4.290	5.674	7.230	9.332	5.156	2.084
0.064	0.083	0.121	0.118	0.145	0.141	0.099
0.310	0.570	0.557	0.835	0.489	0.195	0.092
0.276	0.471	0.430	0.676	0.414	0.151	0.090
0.586	1.040	0.987	1.511	0.903	0.346	0.182
0.104	0.138	0.194	0.526	0.616	0.664	0.567
0.042	0.073	0.145	0.249	0.371	0.710	0.274
0.050	0.045	0.086	0.111	0.242	0.167	0.266
0.076	0.110	0.191	0.272	0.563	0.723	0.554
0.318	0.491	0.650	0.758	0.811	0.490	0.430
0.061	0.133	0.113	0.169	0.196	0.252	0.142
1.161	1.758	2.491	2.749	2.725	2.198	2.506
5.760	8.640	11.520	14.400	17.760	11.520	8.160

Rate (HR).

x $\frac{\text{Organ activity (counts/min)}}{\text{Total injected activity (counts/min) - Activity of blood (counts/min)}}$.

the second half of the arousal process, more and more tissues attain similar blood flow rates in the two groups of bats, and as arousal nears completion definite differences in capillary blood flow concern only brown adipose tissue and stomach. In bats studied during the summer, brown adipose tissue had a lower blood flow and stomach had a higher blood flow.

When capillary flow rates during post-arousal (resting) conditions are compared between winter and summer studies (Fig. 26), differences parallel those found for the blood distribution studies. This is to be expected since cardiac output is similar in these two groups of bats. The most obvious differences are the higher capillary flow rates in anterior muscle and the lower capillary flow rates in brown adipose tissue of post-arousal (resting) bats during the summer.

Estimated nutritional blood flow in anaesthetized, hibernating, and post-arousal (resting) bats is depicted in Figures 34 to 36 and Tables XXV and XXVI. Unlike the differences in organ blood flow between hibernating and post-arousal (resting) bats (Fig. 34), which are mainly due to variations in cardiac output (Tables XXV and XXVI), the differences between anaesthetized and post-arousal (resting) bats (Fig. 34) reflect both the effects of Sodium pentobarbital on the circulation and the alterations in cardiac output. Anterior muscle and kidneys, which receive considerably lower fractions of cardiac output in anaesthetized as compared to post-arousal (resting) bats (Table XIX) also have a noticeably lower blood flow (Fig. 34). Factors responsible for the lower brown fat capillary flow in these animals are the smaller tissue mass (Table V), the relatively smaller fraction of cardiac output received (Table XIX),

and the lower cardiac output (Tables XXV and XXVI). Capillary flow in skin and stomach is relatively high, but in spite of the fact that the myocardium also receives a relatively large fraction of the cardiac output (Table XIX), its capillary flow is lower in anaesthetized than in post-arousal (resting) bats (Fig. 34) because of the smaller cardiac output.

Additional features of interest other than those mentioned previously are not indicated by Figures 35 and 36. Nevertheless, these illustrations are included because they depict the differences in blood flow due to alterations in the distribution of blood and/or in cardiac output (Figs. 27 to 29).

BODY TEMPERATURE

Temperatures of distinct body regions of *E. fuscus*, as measured against heart rate during arousal from hibernation (T_a = 5 C) in winter, are delineated in Figures 37 to 39. All graphs are representations of continuous recordings and in Figure 37 represent average temperatures derived from 20 measurements each. Temperatures of two separate bats are depicted in Figures 38 and 39. Mean values are summarized in Table XXVII. Individual values at different heart rates during arousal, mean values and standard deviations are presented in Appendix 5.

Although body temperatures of *E. fuscus* have been recorded before (Smalley and Dryer, 1963; Hayward *et al.*, 1965), a number of additional features of interest can be seen in Figures 37 to 39. In general, there is a similarity in the shape of the temperature curves of different tissues and body regions. The linearity of the first part of these

Fig. 34. Estimated capillary flow to various organs and tissues in lightly anaesthetized (HR = 340 beats/min; T_a = 22 C) *E. fuscus* in the summer, in deeply hibernating (HR = 12 beats/min; T_a = 5 C) *E. fuscus* in the winter, and in post-arousal (resting; HR = 480 beats/min; T_a = 22 C) *E. fuscus* in the winter. The study is based on the regional distribution of blood (Table XIX) as measured by the 86-Rb (Rubidium) method (Sapirstein, 1958). Flow rate values (Tables XXV and XXVI) are an approximation inasmuch as a constant theoretical stroke volume of 0.024 ml has been assumed (Section: Materials and Methods). Bars were drawn on a 4-cycle semi-logarithmic paper.

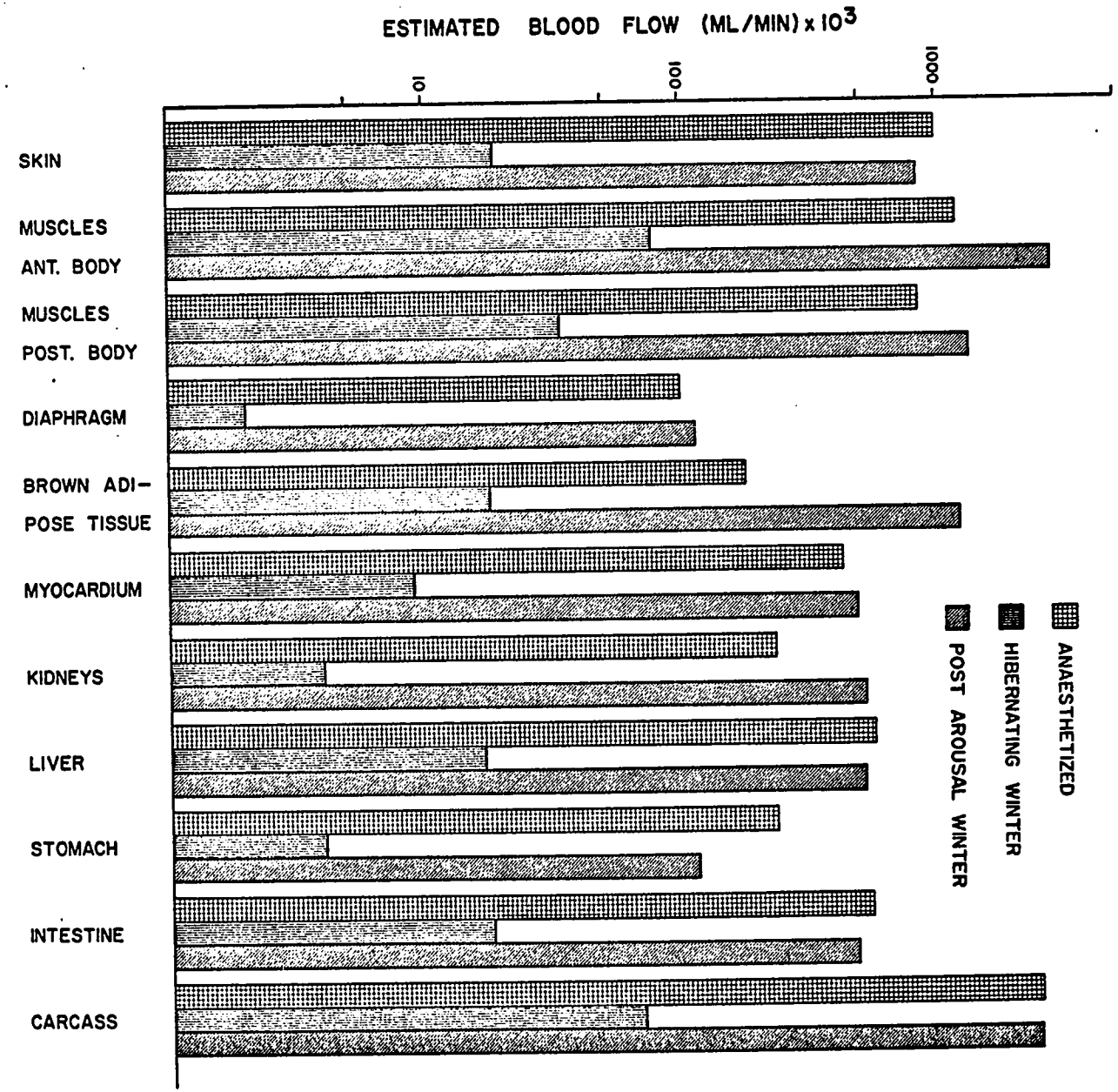

ESTIMATED BLOOD FLOW (ML/MIN) x 10³
10
100
1000
SKIN
MUSCLES ANT. BODY
MUSCLES POST. BODY
DIAPHRAGM
BROWN ADI-POSE TISSUE
MYOCARDIUM
KIDNEYS
LIVER
STOMACH
INTESTINE
CARCASS
ANAESTHETIZED
HIBERNATING WINTER
POST AROUSAL WINTER

Fig. 35. Estimated capillary blood flow to various organs and tissues in lightly anaesthetized (HR = 340 beats/min; T_a = 22 C) *E. fuscus* in the summer and in deeply hibernating (HR = 12 beats/min; T_a = 5 C) *E. fuscus* in the summer and in the winter. The study is based on the regional distribution of blood (Tables XI and XIX) as measured by the 86-Rb (Rubidium) method (Sapirstein, 1958). Flow rate values (Tables XXV and XXVI) are an approximation inasmuch as a constant theoretical stroke volume of 0.024 ml has been assumed (Section: Materials and Methods). Bars were drawn on a 4-cycle semi-logarithmic paper.

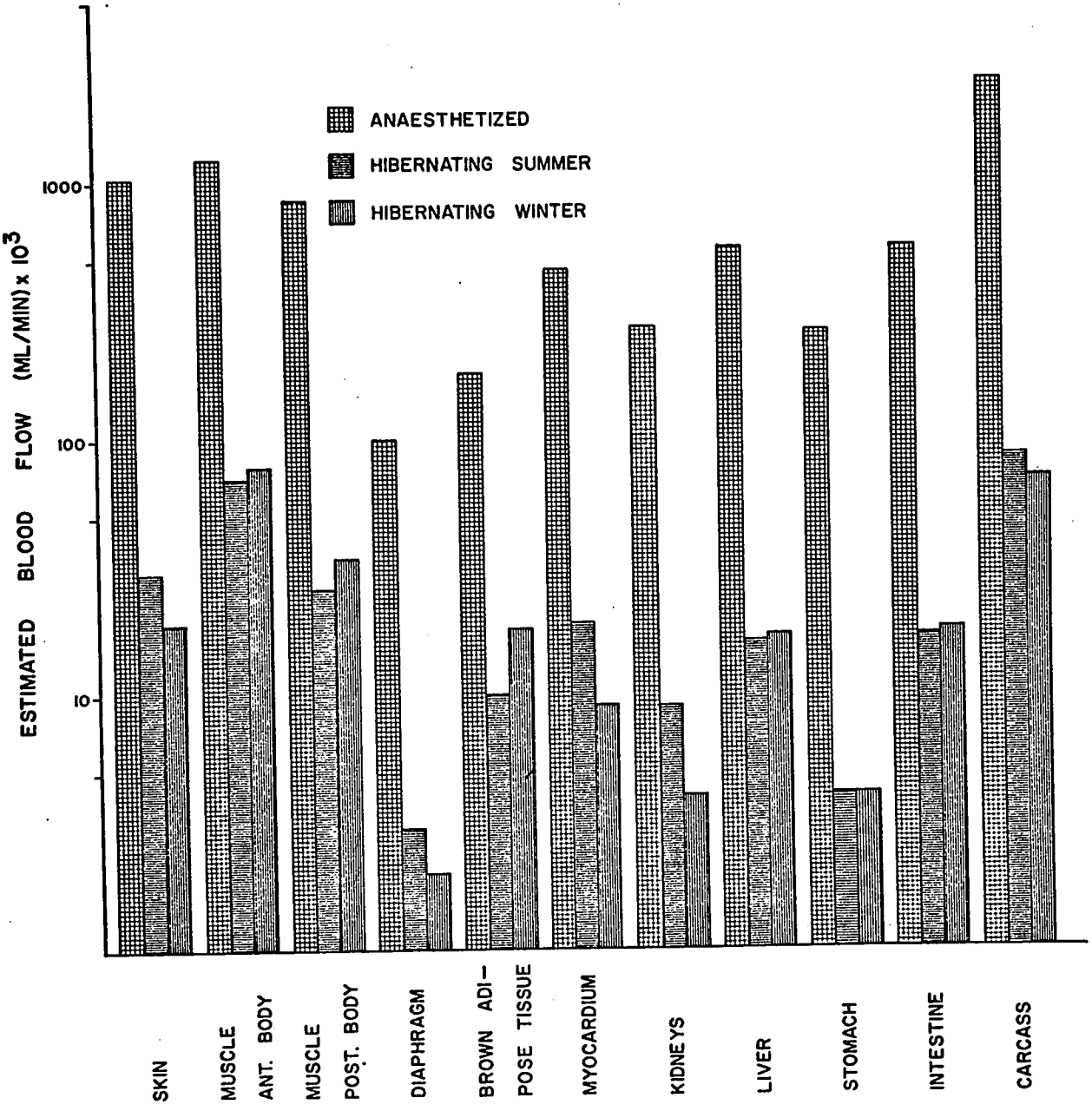
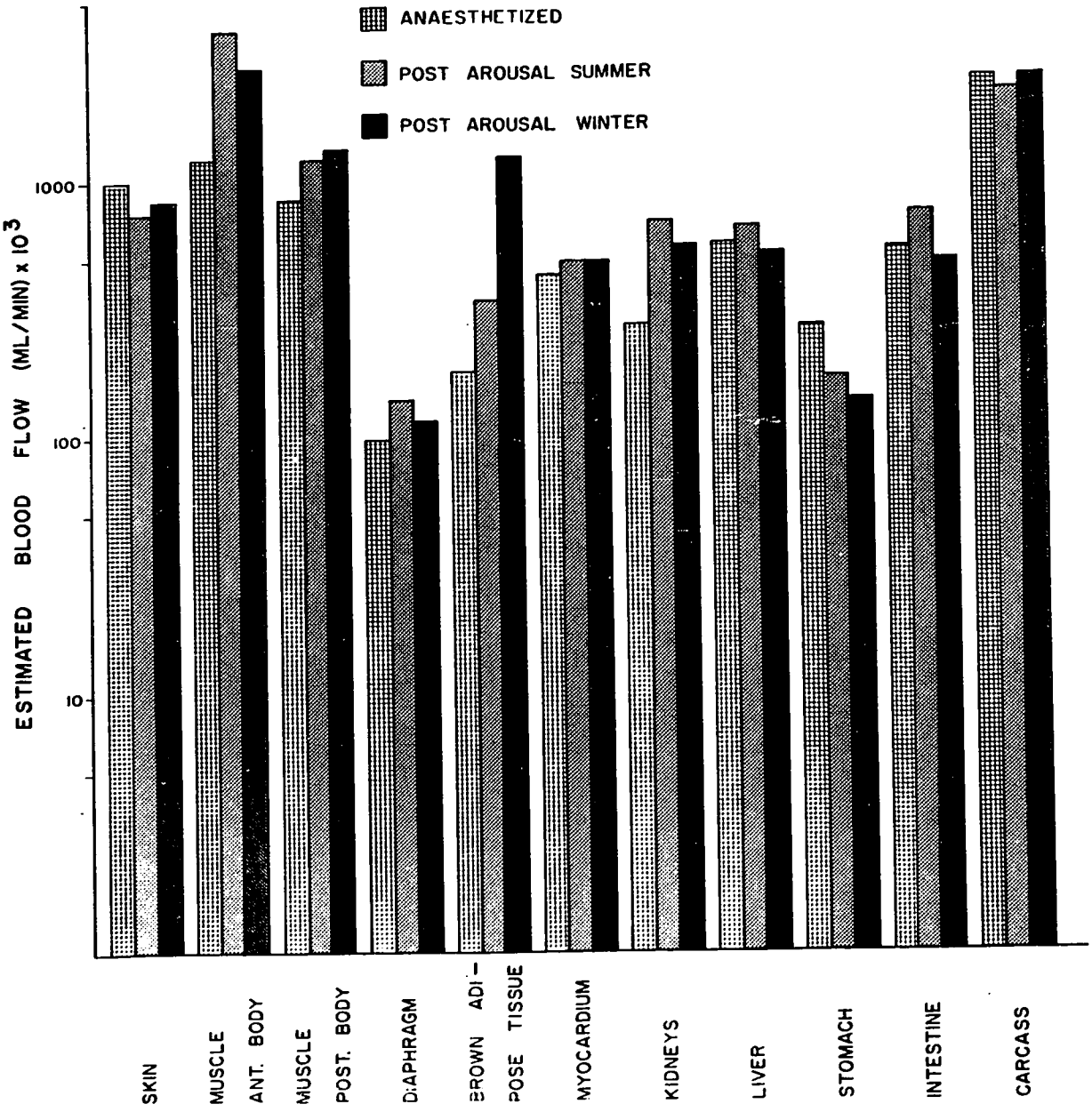

ESTIMATED BLOOD FLOW (ML/MIN) x 10³
1000
100
10
ANAESTHETIZED
HIBERNATING SUMMER
HIBERNATING WINTER
SKIN
MUSCLE ANT. BODY
MUSCLE POST. BODY
DIAPHRAGM
BROWN ADI-POSE TISSUE
MYOCARDIUM
KIDNEYS
LIVER
STOMACH
INTESTINE
CARCASS

Fig. 36. Estimated capillary blood flow to various organs and tissues in lightly anaesthetized (HR = 340 beats/min; T_a = 22 C) *E. fuscus* in the summer and in post-arousal (resting; HR = 480 beats/min; T_a = 22 C) *E. fuscus* in the summer and in the winter. The study is based on the regional distribution of blood (Tables XV and XIX) as measured by the 86-Rb (Rubidium) method (Sapirstein, 1958). Flow rate values (Tables XXV and XXVI) are an approximation inasmuch as a constant theoretical stroke volume of 0.024 ml has been assumed (Section: Materials and Methods). Bars were drawn on a 4-cycle semi-logarithmic paper.

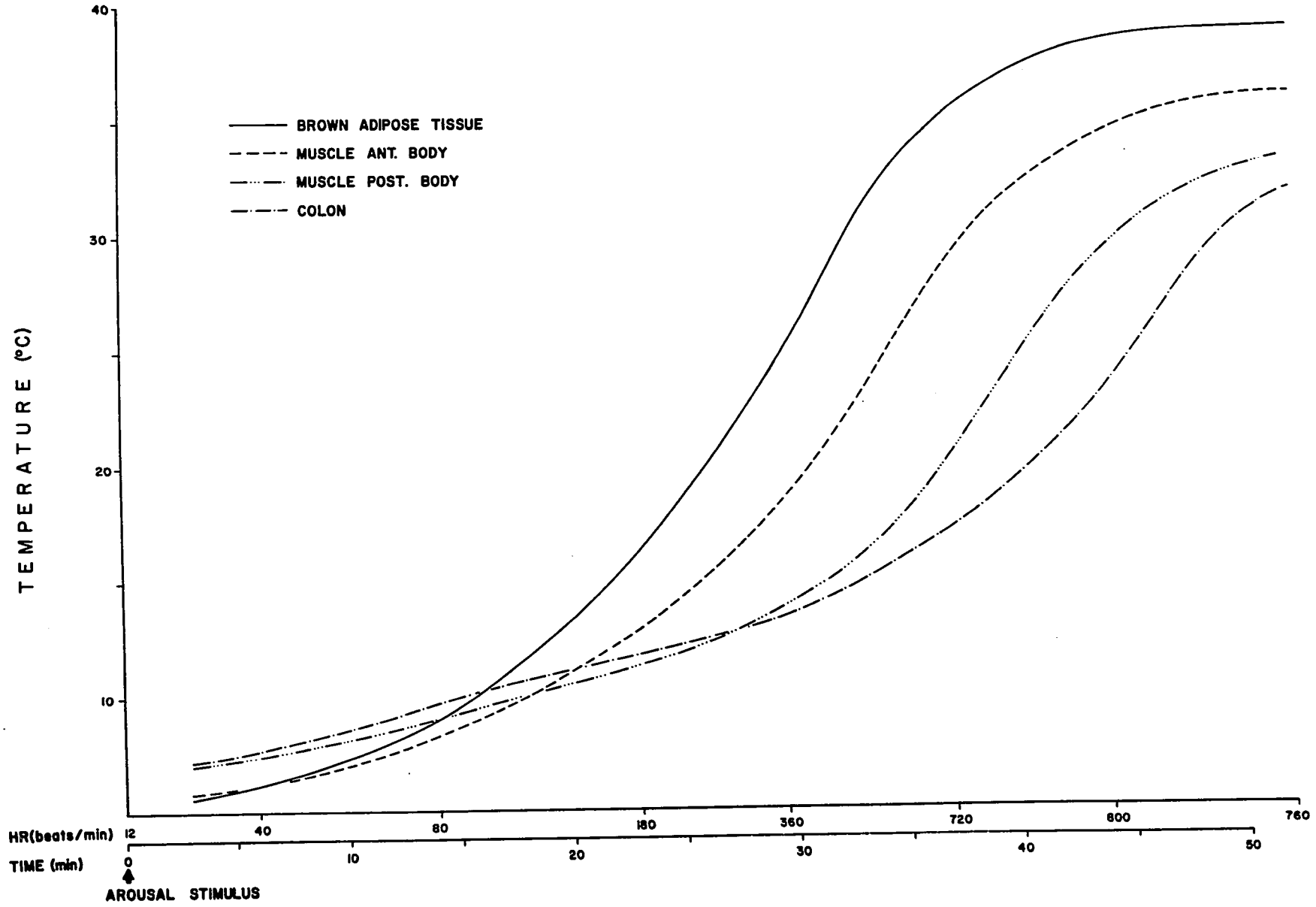

ANAESTHETIZED
POST AROUSAL SUMMER
POST AROUSAL WINTER
ESTIMATED BLOOD FLOW (ML/MIN) x 10³
1000
100
10
SKIN
MUSCLE ANT. BODY
MUSCLE POST. BODY
DIAPHRAGM
BROWN ADI-POSE TISSUE
MYOCARDIUM
KIDNEYS
LIVER
STOMACH
INTESTINE
CARCASS

curves indicates that the temperature increments are fairly constant in early arousal (Fig. 38). The major characteristic during this period of time is a crossing of the temperature curves. This infers that temperature increments differ for different tissues. Brown fat temperature rises more rapidly than do those of other tissues investigated, and that of the colon rises most slowly.

A marked increase in the rate of temperature rise could be observed as a given tissue attained a temperature of about 21 C (Figs. 37 to 39). In most instances, a brief delay preceded the rapid rise in temperature in anterior parts of the body (Figs. 38 and 39). The significance of the inflection in rate of increase of temperature at 21 C is not known. Other workers have found changes at approximately this temperature and these may be related to the observations here. On artificial cooling, rodents incapable of hibernation frequently die of respiratory arrest at about this temperature (Kayser, 1960). The present finding might be a reflection of substrate utilization such as seen by Paulsrud and Dryer (1968) who found that homogenate preparations of bat (*E. fuscus*) brown adipose tissue oxidize palmitate more readily than oleate at temperatures below 20 C. Also, it might be related to the decline in the fraction of cardiac output being delivered to brown fat which starts between heart rates of 240 to 300 beats per minute (Fig. 22), the approximate time when the tissue's temperature reaches 21 C (Fig. 38). Subsequently, brown fat capillary flow begins to decrease at a heart rate of about 480 beats per minute (Fig. 30), even though the tissue's temperature continues to rise. In terms of tissue metabolism and hence heat production, these data are difficult to interpret inasmuch as heat loss by brown adipose tissue to surrounding structures is less above than

Fig. 37. Temperatures of distinct body regions of *E. fuscus* as measured against heart rate during the arousal from hibernation (T_a = 5 C) in the winter. All curves are representations of continuous recordings derived from 20 measurements each. Mean values and standard deviations are presented in Table XXVII.

Fig. 38. Temperatures of distinct body regions of a single *E. fuscus* as measured against heart rate during the arousal from hibernation (T_a = 5 C) in the winter. All curves are representations of continuous recordings. An inflection in rate of increase of temperature at 21 C can be observed in anterior parts of the body.


BROWN ADIPOSE TISSUE
MUSCLE ANT. BODY
MUSCLE POST. BODY
COLON
TEMPERATURE (°C)
40
30
20
10
HR(beats/min)
12
40
80
180
360
720
800
760
TIME (min)
0
10
20
30
40
50
AROUSAL STIMULUS

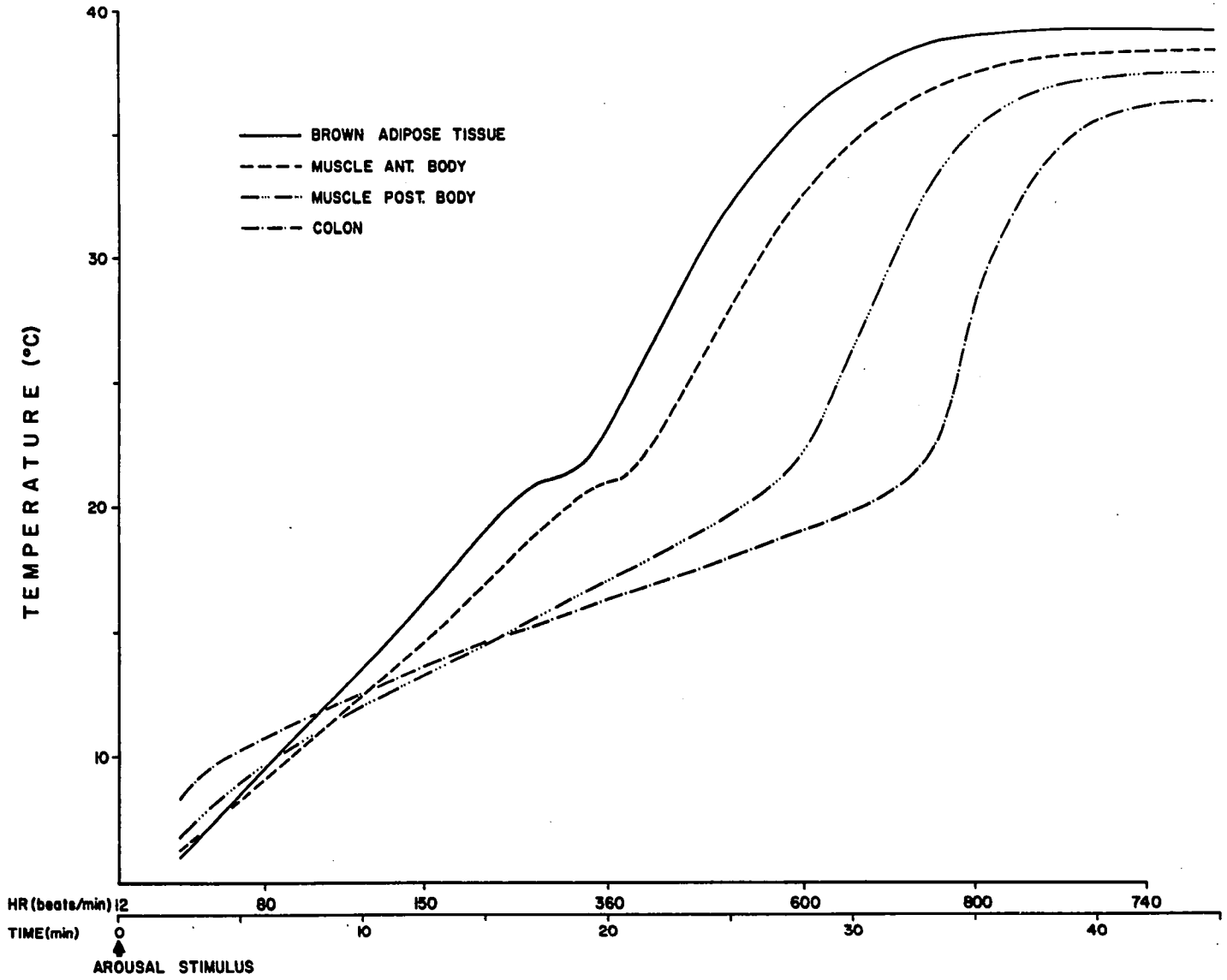
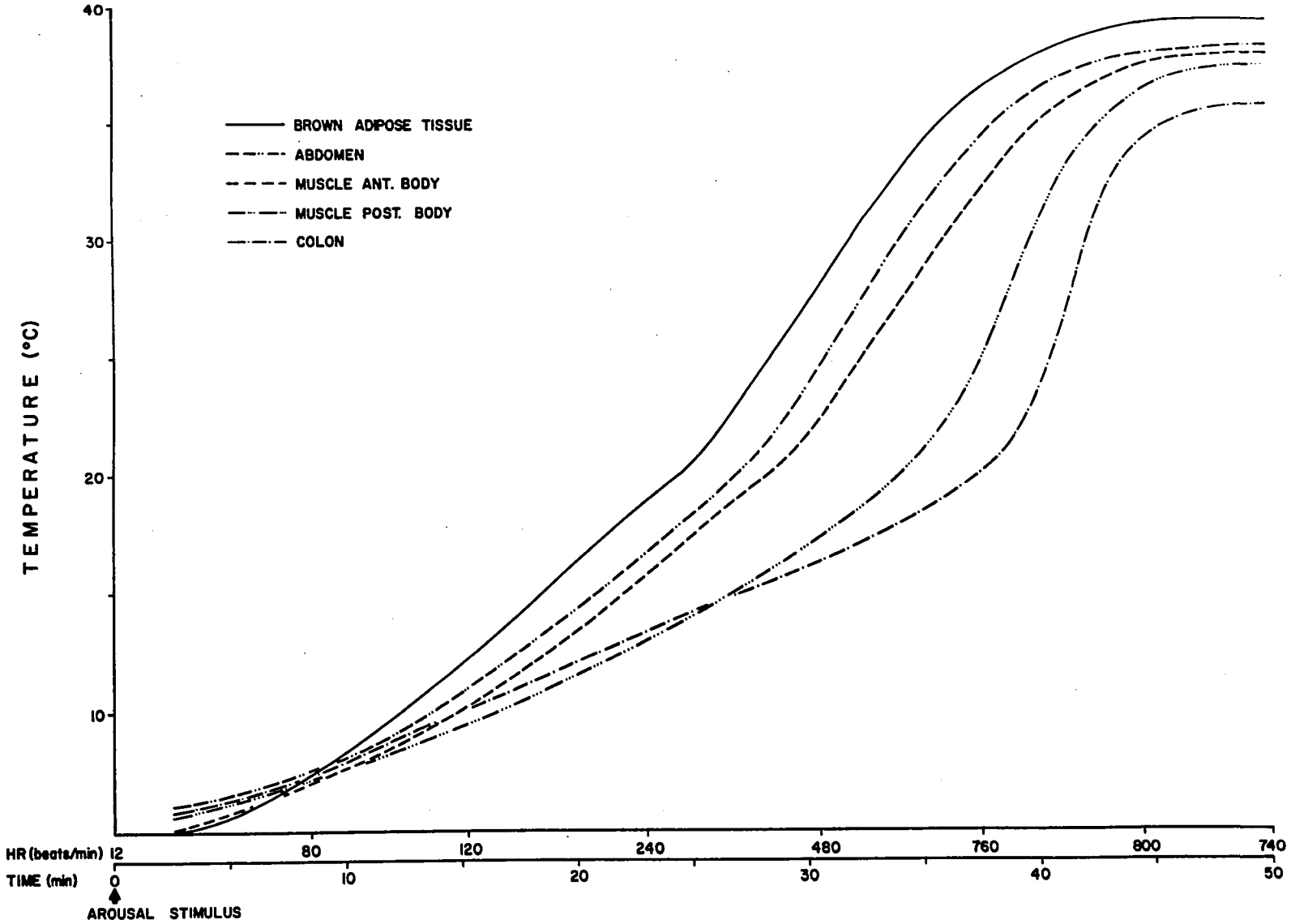

40
30
20
10
TEMPERATURE (°C)
BROWN ADIPOSE TISSUE
MUSCLE ANT. BODY
MUSCLE POST. BODY
COLON
HR (beats/min) 12
80
150
360
600
800
740
TIME (min)
0
10
20
30
40
AROUSAL STIMULUS

Fig. 39. Temperatures of distinct body regions of a single *E. fuscus* as measured against heart rate during the arousal from hibernation (T_a = 5 C) in the winter. All curves are representations of continuous recordings. The abdominal temperature follows and parallels that of brown adipose tissue.


40
30
20
10
TEMPERATURE (°C)
BROWN ADIPOSE TISSUE
ABDOMEN
MUSCLE ANT. BODY
MUSCLE POST. BODY
COLON
HR (beats/min) 12
80
120
240
480
760
800
740
TIME (min) 0
10
20
30
40
50
AROUSAL STIMULUS

it is below 21 C.

The rapid rise in temperature of some other tissues could be largely passive. This is indicated by the abdominal temperature following and paralleling that of brown adipose tissue (Fig. 39) even during early arousal when the increase in nutritional blood flow to the abdominal viscera is limited (Fig. 31). The sharp rise in colonic temperature during late arousal, which is typical of all hibernators investigated, has been attributed to an increasing circulation to posterior body regions (review: Lyman, 1965). The present study supports this conclusion.

DISCUSSION

The sudden metabolic shift that occurs during the arousal from hibernation requires consideration of a series of highly coordinated physiological and biochemical events. This study has dealt only with alterations in the circulation of blood. The importance of circulatory adjustments in arousing hibernators is obvious. Such occurrences as enhanced metabolism, convective heat transfer, and reduced heat loss are dependent upon appropriate adjustments in circulation.

Deep hibernation is characterized by a marked reduction in the metabolic state of the animal. Consequently, important changes in cardiovascular function can be observed. A most obvious alteration is the greatly reduced heart rate which, in *E. fuscus*, averages 12 beats per minute and can be as low as 4 beats per minute. This is a considerable reduction as compared to the average heart rate of 480 beats per minute in post-arousal (resting) bats. All hibernating mammals have similarly low heart rates (reviews: Kayser, 1961; Johansson, 1967). In some instances relatively high values have also been reported, but these are evidently indicative of heart rates in early arousal rather than of those during deep hibernation (review: Johansson, 1967).

A relevant finding in this study is the proportionality with which blood is being distributed throughout the body of deeply hibernating bats. A comparison of weight of organs (Table V) and distribution of blood (Table VI) shows that under the condition of the study the fraction of cardiac output delivered to the majority of organs approximates the fraction of the body weight contributed by these organs and tissues.

This generalization does not apply to the heart and skin. The relatively large fraction of cardiac output delivered to the myocardium probably corresponds to the work load of the heart and the low fraction received by the skin is interpreted as meaning that vasomotor tone in the blood vessels supplying this organ is relatively high during hibernation. This view is strengthened by the fact that under such conditions as anaesthesia the skin receives twice the fraction of the cardiac output it does during hibernation in the winter (Fig. 27). No measurements have been made of the heat loss of hibernating bats but the ability of these animals (as well as that of other hibernators) to survive the winter in the hibernating state is believed to be largely due to a minimization of heat loss resulting from appropriate adjustments in vasomotor tone of the blood vessels supplying the skin and wings.

Unlike the changes that occur in other circulatory variables, there appear to be no major alterations in the distribution of blood between deeply hibernating and post-arousal (resting) bats. The higher fraction of cardiac output received by brown adipose tissue of post-arousal (resting) bats (Fig. 27) is believed to be due to the animals being in a post-arousal condition when they were used in blood distribution studies. Nevertheless, the similarity in the distribution of cardiac output during deep hibernation and during post-arousal (resting) is of interest as it implies that differences in circulation during these physiological conditions are primarily due to differences in the rates of blood flow rather than in the distribution of cardiac output.

Following the onset of arousal from hibernation, there is a sudden increase in heart rate. On several occasions it was observed that

touching a bat in deep hibernation would elicit a two- to fourfold increase in heart rate. Further stimulation (touch) did not produce such a conspicuous change. Heart rates increase slowly during early arousal but accelerate rapidly during the later phase when the heart rate often accelerates by as much as 60 beats per minute per minute. *Eptesicus fuscus* frequently attains a heart rate of about 800 beats per minute during peak arousal. This heart rate is maintained for several minutes following which there is a definite decline (App. 1, Table 2).

The exact sequence in circulatory alterations during initial arousal is difficult to determine, but it seems likely that increased cardiac output, mobilization of venous blood from the splanchnic area, and redistribution of arterial blood commence simultaneously. This rationale takes into consideration the concept that whatever triggers the arousal from hibernation is followed by a massive discharge of the sympathetic nervous system (review: Lyman, 1965; Dryer *et al.*, 1970). Both chronotropic and inotropic responses of the heart to sympathetic nerve stimulation are well documented and substantial evidence indicates that both epinephrine (adrenaline) and norepinephrine (noradrenaline) stimulate brown fat lipolysis (Dryer *et al.*, 1970; review: Lindberg, 1970). Furthermore, these substances produce venoconstriction in the splanchnic area and mobilize blood from this region when the venous pressure is low. At "normal" pressures they increase the distensibility of veins, thus pooling of blood into the venous splanchnic system can occur without significant changes in pressure (see: Grayson and Mendel, 1965). Although these findings relate to non-hibernating mammals, similar occurrences during initial and early arousal must be largely

responsible for an increased venous return in hibernators.

It is generally assumed that norepinephrine (noradrenaline) is the transmitter substance released from sympathetic nerve endings during the initial arousal response. This has been questioned. On the other hand, that arousal is mediated by epinephrine (adrenaline) release is possible. The observed changes in circulation of *E. fuscus* suggest epinephrine (adrenaline) may be the mediator as its effects on the cardiovascular system of hibernating bats are similar to those of non-hibernating mammals. Whereas most of the circulatory changes in arousing hibernators can be explained in terms of norepinephrine (noradrenaline) as the mediator, the administration of this substance to mammalian non-hibernators usually elicits a vasoconstriction in skeletal muscle. The general concept of a predominant metabolic control of the vasculature in skeletal muscle during exercise and a predominant neural control during rest has been suggested to explain the above effect of norepinephrine on these blood vessels in arousing hibernators (Lyman, 1965). It could also be argued that norepinephrine (noradrenaline) is the mediator and that its effect on the vasculature in skeletal muscle is masked by that of a "cholinergic" sympathetic dilator system.

Even though it may not be certain which is the mediator, one may assume that bursts of sympathetic nerve activity, which follow the arousal response, augment the heart rate and cardiac output, increase the tone of the blood vessels of the abdominal viscera and skin, and initiate enhanced brown fat lipolysis. The sudden increase in heart rate results in a translocation of blood from the venous to the arterial side of the circulation which establishes an increased pressure gradient between the

two sides of the system. Blood pressure measurements have not been reported for any hibernator during initial arousal. However, recordings made by Chatfield and Lyman (1950) in the hamster during early arousal have demonstrated sharp rises in the systolic and diastolic pressures which are associated with increasing gradients between these pressures. Similar observations were made in the thirteen-lined ground squirrel (Lyman and O'Brien, 1960) and in the European hedgehog (Kirkebo, 1968). The necessity of a rapid rise in pressure gradients is particularly great in bats which not only encounter the problem of arousing from hibernation in early spring, but which are also confronted with arousing from a daily torpor. Furthermore, the transition from rest to flight requires similar changes. Presumably therefore, *E. fuscus* has the ability to double, triple, or quintuple its heart rate spontaneously under various physiological conditions (Figs. 6 to 9, 15, 18).

The interdependency of cardiac output and venous return is a well established fact. As long as increasing heart rate, force of myocardial contraction, and venous return are coordinated in such a way that cardiac output exceeds peripheral runoff (amount of blood flowing per unit time via the capillary system to the venous side of the circulation), there will be an increase in the difference between mean arterial and venous pressures. Such factors as increasing venomotor tone, decreasing peripheral resistance, increasing ventilation and muscular activity are known to augment venous return, and probably their combined effect accounts for the considerable increments in cardiac output during the arousal process.

The lower arterio-venous pressure gradient in early as compared to late arousal (Chatfield and Lyman, 1950; Lyman and O'Brien, 1960;

Kirkebo, 1968) implies that much of the blood volume resides in capacitance vessels during deep hibernation. In resting mammals, the splanchnic veins serve as a blood reservoir (see: Grayson and Mendel, 1965). In bats which were killed rapidly (present study), the vasculature in the abdomen was observed to be engorged with blood during deep hibernation and rest whereas comparatively small amounts of blood were seen in these vessels during mid-arousal. Similar observations had been made in the European marmot at a much earlier date by Dubois (1896). Because the fraction of the cardiac output delivered to the abdominal viscera declines during early arousal (Fig. 23), the relative but not the absolute amount of blood returning to this region decreases (Fig. 31). Therefore, the blood that is derived from the abdominal area must be largely responsible for the initial increase in cardiac output. With considerably smaller fractions of the increasing cardiac output going to the viscera and skin, the total area circulated per unit time decreases during early arousal. This must be another factor which augments venous return since relatively more blood arrives at the heart per unit time. It follows that an "expanding circulation" during late arousal will be a factor which opposes further increments in cardiac output. Although cardiac output has only been estimated in arousing bats, the studies on the distribution of blood (Figs. 22 to 24) and on heart rates (Figs. 1 to 3) support this view. A similar assumption can be made from the studies performed on the European hedgehog by Kirkebo (1968).

The mechanism underlying the predominantly anterior circulation during the arousal from hibernation has captured the interest of a number of investigators (Johansen, 1961; Bullard and Funkhauser, 1962; Lyman,

1965; Kirkebo, 1968), although it has not been subjected to experimental study. The present investigation demonstrates clearly that the major alterations in circulation between deep hibernation and early arousal (HR = 40 beats/min) are a considerable increment in the fraction of cardiac output delivered to brown adipose tissue, a significant increment of the fraction delivered to anterior muscle, and a considerable decline of it going to the abdominal viscera and skin (Tables XI and XIII). The fractions of cardiac output received by posterior muscle and myocardium are not altered during this period. The findings suggest that in very early arousal, vasomotor tone increases in the blood vessels of the viscera and skin while that of the vasculature in brown adipose tissue and anterior muscle shows a substantial decrease. Such regional alterations in vasomotor tone or local resistance to blood flow must result in a redistribution of blood. The extent to which total peripheral resistance is altered, if at all, during the initial arousal depends upon the sum total of the increasing and decreasing regional resistances. No estimates of peripheral resistance are available for initial arousal, but subsequently the total resistance declines in the arousing European hedgehog and remains constant after mid-arousal (Kirkebo, 1968).

These considerations lead to the following concept. In deep hibernation, heart rate and cardiac output are extremely low, and organ blood flow is thus very limited. Much of the blood volume resides in capacitance vessels, particularly in the splanchnic veins; hence the arterio-venous pressure difference is also reduced. At least in bats, there is no major difference in the distribution of blood between deeply hibernating and resting states. A relatively large fraction of the cardiac

output is delivered to the myocardium, whereas a comparatively small fraction is received by the skin. The resistance of the vasculature of the skin to blood flow not only prevents excessive loss of heat but also aids in maintaining the arterial pressure within reasonable limits.

The initial arousal response and the apparent subsequent firing of the peripheral sympathetic nerves elicit a number of simultaneous events. An augmented heart rate and an increased resistance to blood flow in the abdominal region and skin result in a translocation of blood from the venous to the arterial side of the circulation. The subsequent increasing pressure gradient enhances venous return, particularly that from such regions as the venous splanchnic area. This, in turn, augments cardiac output. Because of the increasing resistance of the vasculature in the abdomen and skin to blood flow and the rapidly increasing demand for oxygen by brown adipose tissue and anterior muscle, increasingly larger fractions of the cardiac output are delivered to anterior body regions. This process is greatly enhanced by the rapid increments in the temperatures of brown adipose tissue, which in *E. fuscus* is confined entirely to anterior body regions.

The fractional delivery of cardiac output to the abdominal viscera and skin in this species continues to decline until near mid-arousal, when a heart rate of about 120 beats per minute is reached. By this time, the fraction of cardiac output to brown adipose tissue shows no further increase but that to the myocardium and diaphragm a definite rise, and that to posterior muscle a significant decline. The reason for the increase to the myocardium is not known, but it might be due to an increase in metabolism. This suggestion is based on the general concept

of a direct relationship between the metabolic activity of the mammalian heart muscle and coronary blood flow. The metabolic rate of the myocardium would also increase as a result of decreasing amounts of cool blood from the posterior and increasing amounts of warm blood from anterior body regions returning to it. This may not be the major reason for the significant increment in the fraction of cardiac output received by the myocardium at a heart rate of about 120 beats per minute. It has been found by Brush (1968) that the myocardium of *E. fuscus* is provided with several isozymes of LDH (lactate dehydrogenase) and esterase, hence one is tempted to speculate that a particular rate-limiting enzyme might be replaced by another which can operate at the higher temperature. The greater demand for oxygen by the diaphragm at about the time when the abdominal viscera and skin receive their lowest fractions of cardiac output and that to brown adipose tissue has become relatively stable, might be partly responsible for the decrease of the fractional delivery of cardiac output to posterior muscle.

The redistribution of blood during the second half of arousal starts with a decline in the fraction of cardiac output going to brown adipose tissue at a heart rate of about 240 to 300 beats per minute when the tissue's temperature is approximately 21 C. This has been demonstrated by Dryer *et al.* (1970) to be the optimum temperature for the *in vitro* oxidation of oleic and palmitic acids by bat (*E. fuscus*) brown adipose tissue homogenates provided succinic acid is present in the medium. These workers also found that in the absence of succinate, the thermal optimum for the oxidation of these substrates occurs at about 30 C. This, in turn, is the temperature at which blood flow to brown

adipose tissue starts to decline and when the rate in temperature increments of this tissue reduces. Furthermore, whereas the fraction of cardiac output delivered to brown adipose tissue begins to decline at a temperature of about 21 C, that to anterior muscle, abdominal viscera, and posterior muscle increases at a similar temperature. Evidently, it is this difference in the metabolic demand for oxygen and the greater heat production by brown adipose tissue, particularly at low temperatures, which largely determine the distribution of blood, and consequently organ blood flow, during the arousal process. All evidence points to the conclusion that during initial arousal the rapid requirement for oxygen by brown adipose tissue is the major reason for the shift in blood flow mainly to anterior body regions, and the rapid rise in the tissue's temperature initiates the warming process. Presumably at temperatures below about 21 C, the rate of aerobic metabolism of most organs is extremely low and determined primarily by the tissue's temperature. At about 21 C, metabolic changes of a presently unknown nature occur. It might be that rate-limiting enzymes are replaced by others that cannot operate below the higher temperatures. Subsequently, the rate of aerobic metabolism rises more rapidly until the thermal optimum for these enzymes is attained. Thus during late arousal the relative blood flow to the abdominal viscera increases more rapidly while blood flow to brown adipose tissue continues to decline and that to anterior muscle becomes maximal. Henceforth, there is a decreasing demand for oxygen by the organs of anterior body regions and an increasing demand by those of the posterior body regions. This results in more and more blood flowing to posterior body regions.

With the removal of the animal from the cold (T_a = 5 C) following peak arousal, heat loss to the environment (T_a = 22 C) is reduced. This

is probably partially responsible for the increased blood flow to the skin during post-arousal (resting) conditions. In any case, with a relatively expanding circulation during late arousal, less blood arrives at the heart per unit time and cardiac output declines. Circulatory parameters readjust in such a way that the distribution of blood is similar to that in deep hibernation, but blood flow proceeds at a considerably higher velocity.

According to a review by Kayser (1961), the majority of hibernators is capable of hibernation only during the winter season. Because bats of the northern hemisphere frequently attain a state which resembles deep hibernation whenever the ambient temperature drops below about 10 C, it has been generally questioned whether or not these heterotherms can hibernate during any season of the year (Kayser, 1961). Menaker (1962) first demonstrated that the ability of *M. lucifugus* to arouse from hibernation in the cold (3 C to 15 C) declines during the spring and increases in fall. None of the bats he investigated were able to arouse between early June and the middle of August. A similar observation was made of *Eptesicus* by Smalley and Dryer (1963) and in the present study.

Menaker (1962) suggested that the inability of *M. lucifugus* to arouse in a cold environment during the summer might be due to insufficient peripheral vasoconstriction and hence to excess heat loss to the environment in an animal with a relatively large surface area. The present investigation provides evidence of a reduced vasomotor tone in the blood vessels supplying the skin, carcass, diaphragm, myocardium, and kidneys of *E. fuscus* subjected to cold (T_a = 5 C) in the summer as compared to the winter. Undoubtedly, the reduced vasomotor tone of peripheral blood

vessels accounts for the correspondingly greater blood flow to the skin and wings (high value for carcass) and a consequently greater heat loss to the environment during induced hibernation in the summer. Furthermore, a reduced vasomotor tone of these blood vessels with little or no compensation elsewhere (Tables XI and XII) infers that the total peripheral resistance is also reduced, which, in turn, results in a decreased pressure difference between mean arterial and venous pressures. If this difference falls below a certain critical level, blood flow comes to a halt.

The relatively large fraction of cardiac output received by the myocardium of bats "hibernating" in the summer, suggests that the work load of the heart is greater in these bats than in the ones hibernating during the natural hibernation season in the winter. Together with the observed haematuria, the findings provide evidence that the high mortality rate (Section: Results) in bats subjected to cold (T_a = 5 C) in the summer is at least partially the consequence of limitations of the circulatory system.

The most obvious limitations of bats arousing from induced hibernation in the summer are the increased blood flow to the skin and the reduced blood flow to brown adipose tissue. This implies that relative heat loss is greater and relative heat production is smaller in these bats as compared to their winter counterparts. Body temperature records of *M. lucifugus* obtained by Menaker (1962) provide evidence of a lower rate of temperature increments during the arousal process in the summer as compared to the winter.

Reduced heat production and excess heat loss are not the only problems these animals encounter. The inability of many bats to elevate

their heart rate much above 120 to 180 beats per minute during the arousal process in the summer is also conspicuous and could relate to limitations of certain metabolic processes in the myocardium of bats subjected to cold (T_a = 5 C) during the summer. Metabolic shifts as are characteristic of rate-limiting enzymes or alternate pathways have been described by a number of investigators (reviews: South and House, 1967; Johansson, 1969) for the myocardium and certain other organs of hibernating mammals as compared to their non-hibernating counterparts. The ability to endure such shifts may be a seasonal phenomenon. Related to this is the observation that the heart of non-hibernating thirteen-lined ground squirrels apparently derives its major energy from carbohydrate metabolism whereas that of hibernating ground squirrels derive it from lipid metabolism (Hawley, 1968). Reduced NAD (nicotinamide adenosine dinucleotide) is required for the catabolism of lipids, an important process during the arousal from hibernation. A major role of LDH (lactate dehydrogenase) is the regulation of cellular NAD^+/NADH ratio (Dawson, 1964) and although their significance is not yet fully appreciated, a number of LDH isozymes have been isolated from the myocardium of *E. fuscus* (Brush, 1968). In addition, greater amounts of inorganic and high energy phosphates are present in the heart muscle of thirteen-lined ground squirrels in September than in May (Zimny *et al.*, 1969). Occasional observations (present study) indicate that large amounts of phosphates are excreted by *E. fuscus* during the first few weeks following the arousal from hibernation in spring. All these findings are noteworthy not because they can explain the differences in cardiac function between bats hibernating in winter and summer, but because they imply that hibernation in *E. fuscus*, as in rodent hibernators, is a

seasonal phenomenon which requires alterations on a cellular level if the animal is to survive in a cold environment.

The arousal from hibernation of *E. fuscus* is a seasonal phenomenon. It involves a sequence of highly coordinated physiological and biochemical events which, within limits, are directed toward an increasingly higher metabolic state of the organism. During this shift, a major role is played by the circulatory system which adjusts nutritional blood flow in various organs and tissues according to the metabolic requirement for oxygen (and other substances) by these organs and tissues. In this study, the redistribution of blood during the arousal process of *E. fuscus* has been determined and capillary blood flow in a variety of organs has been estimated. Haemodynamic principles and the apparent metabolic requirements for oxygen by these organs are apparently major factors governing changes in circulation during the arousal from hibernation.

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A P P E N D I X

APPENDIX 1

HEART RATES (HR) OF *E. FUSCUS* DURING DIFFERENT PHYSIOLOGICAL STATES

Table 1. Heart rates of non-hibernating and hibernating *E. fuscus*

Animal	Non-hibernating (T_a = 22 C)		Hibernating (T_a = 5 C)	
	Non-anaesthetized HR	Lightly anaesthetized HR	Winter HR	Summer HR
1	240	356	12	14
2	300	304	6	12
3	440	366	12	6
4	320	364	14	16
5	280	340	8	14
6	360	320	14	16
7	480	344	16	4
8	260	340	12	12
9	320	320		
10	340	350		
Mean	334	340	12	12
s_d (±)	76	21	3	4

Table 2. Heart rates of *E. fuscus* at 2-minute time intervals

	TIMES (MINUTES)										
	2	4	6	8	10	12	14	16	18	20	22
Animal	Heart										
1	32	38	44	52	62	76	90	106	130	160	200
2	28	36	42	50	60	72	88	104	128	154	184
3	30	34	38	46	56	68	84	100	120	144	174
4	32	36	40	48	56	70	84	98	118	142	174
5	28	34	40	46	54	68	86	100	120	140	180
6	30	34	38	44	50	64	74	98	118	136	176
7	32	38	44	48	56	66	76	94	112	136	162
8	36	40	44	50	60	72	80	96	120	140	170
9	26	30	38	46	58	70	80	96	112	138	168
10	30	36	42	52	64	76	82	106	126	152	184
11	32	38	44	50	56	64	74	84	100	114	134
12	32	38	44	56	68	74	94	110	134	160	194
13	28	34	44	54	64	76	94	110	134	160	200
14	30	34	40	46	52	64	76	88	100	124	148
15	30	34	38	46	54	64	78	98	118	144	172
16	28	32	36	44	52	62	74	94	114	134	164
17	32	38	44	52	62	72	80	96	112	140	160
18	32	38	44	52	62	72	80	100	114	134	154
19	30	36	44	54	64	76	92	104	124	140	170
20	30	34	38	46	54	64	76	88	106	126	154
Mean	30	36	41	49	58	70	82	98	118	141	171
s_d (±)	2	2	3	3	5	5	7	7	10	12	13

during arousal from hibernation in the winter (T_a = 5 C)

DURING AROUSAL											
24	26	28	30	32	34	36	38	40	42	44	46
rates											
244	276	344	500	620	724	780	800	800	800	800	800
224	274	350	486	550	640	710	766	800	800	800	800
210	260	330	420	550	640	710	760	800	800	800	800
206	256	320	400	520	640	720	780	800	800	800	800
220	280	340	400	520	640	720	780	800	800	800	800
216	276	336	400	520	640	720	780	800	800	800	800
202	254	302	400	500	600	700	760	780	800	800	800
200	240	290	350	420	500	620	710	760	780	800	800
198	240	300	360	440	540	620	700	760	780	780	780
224	268	324	414	514	630	704	752	782	800	800	800
160	194	236	290	360	460	620	720	760	800	800	800
234	294	374	474	574	652	724	754	780	800	800	800
250	320	420	560	610	700	750	775	780	800	800	800
184	232	280	380	440	580	674	720	760	780	800	800
204	244	300	380	480	580	680	730	760	790	800	800
184	220	260	320	380	480	560	680	740	780	800	800
180	220	280	360	460	560	620	680	720	760	800	800
174	224	274	364	464	564	624	680	720	760	800	800
200	238	280	360	400	480	600	700	760	790	800	800
190	240	300	380	480	570	660	710	750	780	790	800
205	252	312	398	490	599	676	737	770	790	799	799
23	29	42	62	72	70	57	38	26	14	5	4

Table 3. Heart rates of *E. fuscus* during arousal

	TIMES (MINUTES)															
	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32
ıimal	Heart															
1	20	24	28	32	36	40	52	56	60	72	84	96	108	120	138	152
2	28	32	36	38	42	48	54	60	68	74	80	92	98	120	132	152
3	22	28	36	44	52	58	68	78	86	98	110	124	136	152	176	200
4	30	36	42	48	56	64	72	80	88	96	104	120	128	152	160	176
5	24	28	30	32	38	44	50	56	62	68	74	80	96	104	124	144
6	20	28	32	36	40	42	46	52	60	68	74	80	96	104	124	144
7	18	24	30	36	42	46	52	58	64	76	82	94	106	118	136	160
8	24	28	32	36	42	48	56	64	72	80	88	96	114	126	138	162
9	32	34	36	38	40	42	48	56	64	72	80	88	104	112	128	144
10	24	28	32	36	40	44	48	56	64	72	80	88	100	112	124	148
11	24	28	36	40	48	56	62	66	72	80	86	96	116	126	148	166
12	20	26	34	42	48	56	64	68	74	80	86	92	104	116	132	148
13	28	36	44	48	54	60	64	72	80	88	96	112	120	128	136	148
14	24	30	34	38	42	46	52	58	64	72	80	88	104	120	132	154
15	22	26	32	36	40	48	56	64	76	84	96	104	112	128	144	160
16	20	24	32	36	40	44	48	56	64	72	80	86	92	100	112	124
17	24	32	36	40	44	52	60	66	72	80	86	92	108	124	136	144
18	20	28	34	38	46	54	62	68	80	88	100	112	120	126	132	162
19	18	24	30	34	38	44	48	56	64	72	81	92	104	120	137	158
20	28	32	34	36	42	46	50	56	64	76	80	92	104	120	136	160
lean	24	29	34	38	44	49	56	62	70	78	86	96	108	121	136	155
s_d (±)	4	4	4	4	6	7	8	9	8	9	10	12	11	13	14	15

from hibernation in the summer (T_a = 5 C)

DURING AROUSAL														
34	36	38	40	42	44	46	48	50	52	54	56	58	62	66
rates														
184	218	258	298	358	422	488	520	600	640	680	700	740	760	760
176	200	220	260	300	340	380	440	500	560	600	640	680	740	740
220	240	280	320	360	400	440	480	520	560	600	640	680	740	740
200	216	240	280	320	360	420	480	540	600	646	676	700	720	720
168	200	240	280	320	400	440	480	560	620	660	680	720	780	780
168	200	240	280	320	400	480	560	620	700	740	760	780	800	800
184	220	260	300	360	420	540	620	680	720	740	760	780	780	760
194	218	250	300	350	400	480	560	640	680	720	740	760	760	760
160	200	220	260	300	360	440	520	600	640	680	700	730	760	720
172	196	228	268	320	360	420	480	560	640	680	720	760	720	700
200	254	306	380	440	480	560	620	660	680	720	740	780	780	760
172	196	216	232	260	300	360	400	480	560	600	640	680	740	760
160	172	196	220	260	300	360	400	440	520	560	640	720	780	780
166	198	238	280	320	360	400	420	470	530	560	600	640	700	740
184	208	240	280	320	360	420	500	560	640	680	740	760	780	780
136	148	172	196	228	268	320	360	420	480	560	640	680	740	760
160	180	200	220	240	272	300	320	360	400	480	540	560	640	760
174	194	224	276	304	320	340	380	440	520	570	640	680	740	720
184	214	247	288	340	380	420	440	460	520	580	640	676	724	740
180	200	240	280	300	360	380	460	520	580	640	680	720	760	760
177	204	236	275	316	363	419	476	532	589	635	676	711	747	752
18	23	29	40	48	53	68	81	86	81	72	58	55	36	25

APPENDIX 2

ORGAN, TISSUE, AND BODY WEIGHTS OF *E. FUSCUS*, SACRIFICED DURING DIFFERENT PHYSIOLOGICAL STATES, AND DIFFERENT SEASONS OF THE YEAR

Table 1. Organ, tissue, and body weights (grams) of non-hibernating, lightly anaesthetized *E. fuscus*, sacrificed in the summer

	Group A					
	1a	2a	3a	4a	5a	6a
Skin	2.2235	1.9660	2.2031	2.1247	2.1362	1.7082
Muscle ant. body	3.6498	4.1797	3.3913	3.8530	3.5974	3.9285
Muscle post. body	1.2268	1.3220	1.0686	1.0843	1.2321	1.4083
Total muscle	4.8766	5.5017	4.4599	4.9373	4.8295	5.3368
Diaphragm	0.0949	0.1061	0.0808	0.0894	0.0842	0.1092
Interscap. B.A.T.	0.4583	0.5090	0.2590	0.1821	0.3298	0.0952
Other B.A.T.	0.3735	0.4499	0.2716	0.2544	0.3857	0.1923
Total B.A.T.	0.8318	0.9589	0.5306	0.4365	0.7155	0.2875
Liver	0.6659	0.6659	0.6714	0.6391	0.7355	0.8438
Kidneys	0.1432	0.1426	0.1151	0.1481	0.1483	0.1617
Stomach	0.2052	0.1639	0.2047	0.1577	0.1896	0.2073
Intestine	0.3173	0.4122	0.2611	0.3301	0.3112	0.2499
Myocardium	0.1109	0.1375	0.1035	0.1311	0.1153	0.1269
Blood	1.0723	1.0217	0.9530	1.1409	1.1667	1.0496
W.A.T.	4.3944	2.9531	1.0509	0.6804	0.7370	1.0548
Carcass	4.8135	5.1587	5.3076	5.5950	5.2483	5.2339
Total body wt.	19.7495	19.1883	15.9417	16.4103	16.4173	16.3696
Semilean body wt.	15.3551	16.2352	14.8908	15.7299	15.6803	15.3148
Lean body wt.	14.5233	15.2763	14.3602	15.2934	14.9648	15.0273

	7a	8a	9a	10a	Mean	s_d (±)
Skin	2.1159	1.9176	1.3356	2.1847	1.9916	0.0785
Muscle ant. body	5.0415	4.8231	4.0254	4.8079	4.1298	0.5736
Muscle post. body	1.4963	1.6089	1.3793	1.5193	1.3346	0.1814
Total muscle	6.5378	6.4320	5.4047	6.3272	5.4644	0.7371
Diaphragm	0.1002	0.1244	0.0976	0.1166	0.1000	0.0140
Interscap. B.A.T.	0.1949	0.2624	0.1616	0.1827	0.2635	0.1575
Other B.A.T.	0.1816	0.2538	0.1596	0.1861	0.2709	0.1000
Total B.A.T.	0.3765	0.5162	0.3212	0.3688	0.5344	0.2286
Liver	0.7010	0.7787	0.5479	0.7726	0.7022	0.0840
Kidneys	0.1543	0.1669	0.1698	0.1920	0.1542	0.0204
Stomach	0.1638	0.1945	0.1543	0.1748	0.1816	0.0210
Intestine	0.3833	0.4989	0.2974	0.3363	0.3398	0.0745
Myocardium	0.1266	0.1552	0.1283	0.1540	0.1289	0.0169
Blood	1.1423	1.1135	1.0619	1.1568	1.0878	0.0686
W.A.T.	0.9155	1.6094	0.7370	0.9560	1.5089	1.2190
Carcass	6.1088	5.5445	5.3967	6.0415	5.4270	0.3807
Total body wt.	18.8260	19.0518	15.6524	18.7813	17.6388	1.5988
Semilean body wt.	17.9105	17.4424	14.9154	17.8253	16.1300	1.1745
Lean body wt.	17.5340	16.9262	14.5942	17.4565	15.5956	1.2285

Table 2. Organ and tissue weights (expressed as a percentage of semilean body weight) of non-hibernating, lightly anaesthetized *E. fuscus*, sacrificed in the summer

	Group A					
	1a	2a	3a	4a	5a	6a
Skin	14.48	12.11	14.78	13.51	13.62	11.15
Muscle ant. body	23.77	25.74	22.17	24.49	22.94	25.65
Muscle post. body	7.99	8.14	7.18	6.93	7.86	9.20
Total muscle	31.76	33.88	29.95	31.42	30.80	34.85
Diaphragm	0.61	0.65	0.54	0.56	0.54	0.71
Interscap. B.A.T.	2.98	3.13	3.56	1.16	2.10	0.62
Other B.A.T.	2.43	2.77	1.82	1.62	2.50	1.26
Total B.A.T.	5.41	5.90	5.38	2.78	4.60	1.88
Liver	4.34	4.10	4.51	4.06	4.69	5.51
Kidneys	0.93	0.87	0.77	0.94	0.94	1.06
Stomach	1.34	1.00	1.37	1.00	1.21	1.35
Intestine	2.07	2.54	1.75	2.10	1.98	1.63
Myocardium	0.72	0.85	0.70	0.83	0.74	0.83
Blood	6.98	6.29	6.40	7.25	7.44	6.85
Carcass	31.34	31.77	35.64	35.60	33.47	34.18
	7a	8a	9a	10a	Mean	s_d (±)
Skin	11.81	10.99	8.95	12.26	12.37	1.78
Muscle ant. body	28.15	27.65	26.99	26.97	25.45	2.05
Muscle post. body	8.35	9.22	9.25	8.52	8.26	0.82
Total muscle	36.50	36.87	36.24	35.49	33.71	2.59
Diaphragm	0.56	0.71	0.65	0.65	0.62	0.06
Interscap. B.A.T.	1.09	1.50	1.08	1.02	1.82	1.05
Other B.A.T.	1.01	1.46	1.07	1.04	1.70	0.66
Total B.A.T.	2.10	2.96	2.15	2.06	3.52	1.61
Liver	3.91	4.46	3.67	4.33	4.36	0.50
Kidneys	0.86	0.96	1.14	1.08	0.96	0.11
Stomach	0.91	1.12	1.03	0.98	1.13	0.17
Intestine	2.14	2.86	1.99	1.87	2.09	0.36
Myocardium	0.71	0.89	0.86	0.86	0.80	0.07
Blood	6.38	6.38	7.12	6.49	6.76	0.42
Carcass	34.11	31.79	36.18	33.89	33.80	1.73

Table 3. Organ and tissue weights (expressed as a percentage of lean body weight) of non-hibernating, lightly anaesthetized *E. fuscus*, sacrificed in the summer

	Group A					
	1a	2a	3a	4a	5a	6a
Skin	15.31	12.87	15.34	13.89	14.27	11.37
Muscle ant. body	25.13	27.36	22.99	25.19	24.04	26.14
Muscle post. body	8.45	8.65	7.34	7.12	8.23	9.37
Total muscle	33.58	36.01	30.33	32.31	32.27	35.51
Diaphragm	0.65	0.69	0.56	0.58	0.56	0.73
Liver	4.59	4.36	4.68	4.18	4.92	5.62
Kidneys	0.97	0.93	0.80	0.97	0.99	1.08
Stomach	1.41	1.07	1.42	1.03	1.27	1.38
Intestine	2.18	2.70	1.82	2.16	2.08	1.66
Myocardium	0.76	0.90	0.72	0.86	0.77	0.84
Blood	7.38	6.69	6.64	7.46	7.80	6.98
Carcass	33.14	33.77	36.96	36.58	35.07	34.83
	7a	8a	9a	10a	Mean	s_d (±)
Skin	12.07	11.33	9.15	12.52	12.81	1.95
Muscle ant. body	28.75	28.49	27.58	27.54	26.32	1.94
Muscle post. body	8.53	9.51	9.45	8.70	8.54	0.80
Total muscle	37.28	38.00	37.03	36.24	34.86	2.57
Diaphragm	0.57	0.73	0.66	0.67	0.64	0.07
Liver	4.00	4.60	3.75	4.43	4.51	0.52
Kidneys	0.88	0.99	1.16	1.10	0.99	0.11
Stomach	0.93	1.15	1.06	1.00	1.17	0.18
Intestine	2.19	2.95	2.04	1.93	2.17	0.39
Myocardium	0.72	0.92	0.88	0.88	0.82	0.08
Blood	6.51	6.58	7.28	6.63	6.99	0.45
Carcass	34.84	32.76	36.98	34.61	34.74	1.51

Table 4. Organ, tissue, and body weights (grams) of *E. fuscus*, sacrificed at different heart rates during arousal from hibernation in the winter

	Group B				
	1b	2b	3b	4b	5b
Skin	1.8623	1.7270	1.8748	1.6450	1.5766
Muscle ant. body	3.9192	4.0990	4.0556	3.6510	3.5117
Muscle post. body	1.5097	1.5454	1.3640	1.5215	1.4112
Total muscle	5.4289	5.6444	5.4196	5.1725	4.9229
Diaphragm	0.0963	0.1057	0.1019	0.1025	0.0975
Interscap. B.A.T.	0.4340	0.5140	0.5444	0.4176	0.5364
Other B.A.T.	0.3858	0.4608	0.6426	0.3884	0.5223
Total B.A.T.	0.8198	0.9748	1.1870	0.8060	1.0587
Liver	0.8095	0.8002	0.7207	0.6347	0.5655
Kidneys	0.1877	0.1705	0.1427	0.1204	0.1568
Stomach	0.1183	0.1356	0.1244	0.1305	0.1399
Intestine	0.5264	0.7513	0.5832	0.6445	0.5945
Myocardium	0.1320	0.1306	0.1261	0.1270	0.1573
Blood	1.4186	1.4556	1.4278	1.3362	1.3735
W.A.T.	0.5166	1.3192	5.0451	2.0377	2.6480
Carcass	5.6160	5.5964	5.1531	5.0758	5.1230
Total body wt.	17.5324	18.8113	21.9064	17.8328	18.4142
Semilean body wt.	17.0158	17.4921	16.8613	15.7951	15.7662
Lean body wt.	16.1960	16.5173	15.6743	14.9891	14.7075
	6b	7b	8b	9b	10b
Skin	1.9705	2.3994	2.2198	2.9709	1.6496
Muscle ant. body	4.2605	4.2750	4.4240	4.6136	3.9915
Muscle post. body	1.6612	1.6873	1.5524	1.7682	1.3865
Total muscle	5.9217	5.9623	5.9764	6.3818	5.3780
Diaphragm	0.1238	0.1209	0.1181	0.1370	0.1060
Interscap. B.A.T.	0.5896	0.4519	0.5439	0.5141	0.4163
Other B.A.T.	0.4944	0.4717	0.4687	0.4584	0.4138
Total B.A.T.	1.0840	0.9236	1.0126	0.9725	0.8301
Liver	0.7515	0.8553	0.8935	0.8547	0.7493
Kidneys	0.1881	0.2160	0.1873	0.2256	0.1602
Stomach	0.2070	0.1238	0.1426	0.2061	0.1281
Intestine	0.5171	0.5926	0.6736	0.7359	0.6207
Myocardium	0.1425	0.1647	0.1726	0.1756	0.1287
Blood	1.5187	1.6260	1.8944	1.6263	1.7314
W.A.T.	3.7376	6.2069	5.9984	5.7759	4.4617
Carcass	6.4710	6.4386	6.4700	6.3197	5.2638
Total body wt.	22.6335	25.6301	25.7593	26.3820	21.2076
Semilean body wt.	18.8959	19.4232	19.7609	20.6061	16.7459
Lean body wt.	17.8119	18.4996	18.7483	19.6336	15.9158

Table 4 (continued)

	Group B				
	11b	12b	13b	14b	15b
Skin	1.6053	1.6733	1.7946	1.5646	2.2178
Muscle ant. body	3.8739	3.7413	3.4715	3.5187	4.2869
Muscle post. body	1.4572	1.4502	1.4538	1.3628	1.5973
Total muscle	5.3311	5.1915	4.9253	4.8815	5.8842
Diaphragm	0.0959	0.0905	0.1066	0.1131	0.1246
Interscap. B.A.T.	0.5860	0.5581	0.4798	0.4864	0.4417
Other B.A.T.	0.4715	0.5126	0.4612	0.4474	0.3716
Total B.A.T.	1.0575	1.0707	0.9410	0.9338	0.8133
Liver	0.6567	0.7402	0.6541	0.5401	0.9115
Kidneys	0.1782	0.1203	0.1867	0.1811	0.2125
Stomach	0.1515	0.1234	0.1336	0.1278	0.1534
Intestine	0.5226	0.3954	0.6077	0.5513	0.7117
Myocardium	0.1526	0.1310	0.1554	0.1277	0.1592
Blood	1.4512	1.3568	1.5767	1.4307	1.8413
W.A.T.	2.5666	4.4944	4.0441	3.7267	6.7276
Carcass	6.0446	5.3069	5.4058	5.0836	5.9533
Total body wt.	19.8138	20.6944	20.5316	19.2620	25.7104
Semilean body wt.	17.2472	16.2000	16.4875	15.5353	18.9828
Lean body wt.	16.1897	15.1293	15.5465	14.6015	18.1695
	16b	17b	18b	19b	20b
Skin	1.9249	1.4009	1.8707	1.5865	1.9760
Muscle ant. body	3.5067	3.2562	3.2064	3.1801	3.7952
Muscle post. body	1.1525	1.2860	1.3979	1.1004	1.4450
Total muscle	4.6592	4.5422	4.6043	4.2805	5.2402
Diaphragm	0.0785	0.1208	0.0855	0.0947	0.1243
Interscap. B.A.T.	0.4532	0.4129	0.5684	0.4077	0.4654
Other B.A.T.	0.4443	0.4099	0.5060	0.4045	0.4162
Total B.A.T.	0.8975	0.8228	1.0744	0.8122	0.8816
Liver	0.6660	0.4063	0.7800	0.4342	0.6371
Kidneys	0.1725	0.1258	0.1246	0.1155	0.1962
Stomach	0.1305	0.1224	0.1370	0.1270	0.1187
Intestine	0.6075	0.4181	0.3620	0.4195	0.5283
Myocardium	0.1444	0.1146	0.1331	0.1142	0.1243
Blood	1.2100	1.6002	1.3738	1.1148	1.5760
W.A.T.	4.2712	4.1340	3.8997	3.8324	7.4325
Carcass	4.9550	4.9201	5.0398	4.5321	5.1889
Total body wt.	19.7172	18.7282	19.4849	17.4636	24.0241
Semilean body wt.	15.4460	14.5942	15.5852	13.6312	16.5916
Lean body wt.	14.5485	13.7714	14.5108	12.8190	15.7100

Table 4 (continued)

	Group B				
	21b	22b	23b	24b	25b
Skin	2.5944	1.8781	2.0299	2.1331	1.6676
Muscle ant. body	3.9175	3.4017	3.9086	4.3820	3.7416
Muscle post. body	1.4200	1.2446	1.5427	1.6533	1.4460
Total muscle	5.3375	4.6463	5.4513	6.0353	5.1876
Diaphragm	0.1250	0.0899	0.1152	0.1354	0.0990
Interscap. B.A.T.	0.4667	0.4744	0.3300	0.4682	0.5640
Other B.A.T.	0.3613	0.4171	0.4165	0.4305	0.4059
Total B.A.T.	0.8280	0.8915	0.7465	0.8987	0.9699
Liver	0.9400	0.6204	0.9469	0.5967	0.6548
Kidneys	0.1845	0.1585	0.2429	0.2016	0.1172
Stomach	0.1244	0.1151	0.1495	0.1196	0.0915
Intestine	0.5802	0.4370	0.6498	0.5555	0.4749
Myocardium	0.1642	0.1241	0.1750	0.1614	0.1209
Blood	1.7542	1.3942	1.5588	1.3797	1.1532
W.A.T.	8.6790	6.4190	3.7908	7.0907	4.3029
Carcass	5.5093	5.0522	6.1393	6.0136	4.9397
Total body wt.	26.8207	21.8263	21.9959	25.3213	19.7792
Semilean body wt.	18.1417	15.4073	18.2051	18.2306	15.4763
Lean body wt.	17.3137	14.5158	17.4586	17.3319	14.5064
	26b	27b	28b	29b	30b
Skin	2.2486	2.3841	1.8230	2.2136	1.9251
Muscle ant. body	4.2365	4.5576	3.3796	4.2144	3.8415
Muscle post. body	1.5756	1.6674	1.1177	1.5408	1.4370
Total muscle	5.8121	6.2250	4.4973	5.7552	5.2785
Diaphragm	0.1263	0.1280	0.0973	0.1272	0.1157
Interscap. B.A.T.	0.5831	0.6385	0.4526	0.5750	0.3528
Other B.A.T.	0.5918	0.6599	0.4680	0.5373	0.4189
Total B.A.T.	1.1749	1.2984	0.9206	1.1123	0.7717
Liver	0.9183	0.8777	0.5185	0.8705	0.9256
Kidneys	0.2205	0.1980	0.1825	0.1669	0.1680
Stomach	0.1432	0.1445	0.1122	0.1412	0.1409
Intestine	0.5142	0.5862	0.4307	0.7510	0.5737
Myocardium	0.1951	0.1816	0.1337	0.1772	0.1597
Blood	1.4175	1.4113	1.2742	1.3479	1.5346
W.A.T.	7.0376	6.2513	3.6600	5.4103	6.4165
Carcass	6.2163	6.8080	5.0151	6.4152	5.3410
Total body wt.	26.0246	26.4941	18.6651	24.4885	23.3510
Semilean body wt.	18.9870	20.2428	15.0051	19.0782	16.9345
Lean body wt.	17.8121	18.9444	14.0845	17.9659	16.1628

Table 4 (continued)

	Group B				
	31b	32b	33b	34b	35b
Skin	2.1486	1.9860	1.8891	3.4380	1.8079
Muscle ant. body	3.8630	3.8047	3.3517	4.6345	3.6475
Muscle post. body	1.4702	1.6156	1.2107	1.5719	1.2928
Total muscle	5.3332	5.4203	4.5624	6.2064	4.9403
Diaphragm	0.1177	0.1109	0.0920	0.1088	0.1046
Interscap. B.A.T.	0.3931	0.5007	0.4048	0.3340	0.4444
Other B.A.T.	0.4003	0.5648	0.4681	0.2847	0.4813
Total B.A.T.	0.7934	1.0655	0.8729	0.6187	0.9257
Liver	0.7050	0.6627	0.4189	0.6775	0.6300
Kidneys	0.1722	0.1464	0.1369	0.2227	0.2004
Stomach	0.1661	0.1869	0.0870	0.1372	0.1253
Intestine	0.6871	0.5052	0.4620	0.7919	0.7847
Myocardium	0.1513	0.1873	0.1150	0.1543	0.1617
Blood	1.3910	1.5010	1.0517	1.6551	1.4425
W.A.T.	5.4475	6.0965	3.2522	4.9340	6.7543
Carcass	5.6006	5.3355	4.9203	6.2738	5.4626
Total body wt.	22.7137	23.2042	17.8604	25.2184	23.3400
Semilean body wt.	17.2662	17.1077	14.6082	20.2844	16.5857
Lean body wt.	16.4728	16.0422	13.7353	19.6657	15.6600
	36b	37b	38b	39b	40b
Skin	2.1175	2.0513	1.8427	2.2424	1.4592
Muscle ant. body	3.7669	3.6494	3.2742	4.2425	3.1770
Muscle post. body	1.3771	1.2918	1.1590	1.7967	1.3326
Total muscle	5.1440	4.9412	4.4332	6.0392	4.5096
Diaphragm	0.1117	0.1044	0.0933	0.1169	0.0980
Interscap. B.A.T.	0.5181	0.4921	0.3976	0.5620	0.4820
Other B.A.T.	0.4330	0.4105	0.3519	0.4605	0.4936
Total B.A.T.	0.9511	0.9026	0.7495	1.0225	0.9756
Liver	0.6402	0.6312	0.5438	0.6228	0.6141
Kidneys	0.1441	0.1686	0.2577	0.1797	0.1505
Stomach	0.1364	0.1349	0.1098	0.1012	0.1226
Intestine	0.6027	0.6251	0.3263	0.4967	0.4235
Myocardium	0.1218	0.1250	0.1049	0.1657	0.1232
Blood	1.2119	1.2040	1.2526	1.4959	1.2476
W.A.T.	5.0350	1.0797	2.5664	5.6138	4.7333
Carcass	5.3100	4.9933	4.6433	5.9245	4.7023
Total body wt.	21.5264	16.9613	16.9235	24.0213	19.1595
Semilean body wt.	16.4914	15.8816	14.3571	18.4075	14.4262
Lean body wt.	15.5403	14.9790	13.6076	17.3850	13.4506

Table 4 (continued)

	Group B				
	41b	42b	43b	44b	45b
Skin	1.9814	2.4149	1.7619	2.0663	2.5638
Muscle ant. body	3.9385	4.3083	3.7320	4.6427	4.1979
Muscle post. body	1.4640	1.5818	1.4172	1.5912	1.6608
Total muscle	5.4025	5.8901	5.1492	6.2339	5.8587
Diaphragm	0.1360	0.1209	0.1093	0.1145	0.1437
Interscap. B.A.T.	0.3985	0.5793	0.5452	0.4857	0.7830
Other B.A.T.	0.3856	0.5674	0.6262	0.4207	0.4547
Total B.A.T.	0.7841	1.1467	1.1714	0.9064	1.2377
Liver	0.6234	0.8461	0.5379	0.6402	0.7270
Kidneys	0.1655	0.2247	0.1328	0.1523	0.2003
Stomach	0.1498	0.1275	0.1262	0.1246	0.1261
Intestine	0.5809	0.5410	0.4475	0.4976	0.6195
Myocardium	0.1211	0.1374	0.1556	0.1560	0.1631
Blood	1.5180	1.5378	1.3026	1.4658	1.2738
W.A.T.	4.9530	7.3835	5.2166	5.9767	9.9540
Carcass	5.5345	5.4975	5.2640	5.4335	5.2701
Total body wt.	21.9502	25.8681	21.3750	23.7678	28.1378
Semilean body wt.	16.9972	18.4846	16.1584	17.7911	18.1838
Lean body wt.	16.2131	17.3379	14.9870	16.8847	16.9461
	46b	47b	48b	49b	50b
Skin	1.5502	2.0216	1.7034	1.4819	2.2334
Muscle ant. body	3.8854	4.1403	3.4320	5.1267	4.0406
Muscle post. body	1.4747	1.5472	1.3811	1.1380	1.5066
Total muscle	5.3601	5.6875	4.8131	6.2647	5.5472
Diaphragm	0.1204	0.1370	0.1075	0.0942	0.1206
Interscap. B.A.T.	0.4656	0.6944	0.6001	0.4618	0.6439
Other B.A.T.	0.4239	0.5657	0.6495	0.5204	0.6080
Total B.A.T.	0.8895	1.2601	1.2496	0.9822	1.2519
Liver	0.6278	0.7550	0.8413	0.6453	0.7983
Kidneys	0.1526	0.2323	0.2012	0.1799	0.1787
Stomach	0.1420	0.1374	0.1860	0.1359	0.1010
Intestine	0.5845	0.4574	0.6847	0.4780	0.6687
Myocardium	0.1339	0.1560	0.1542	0.1161	0.1542
Blood	1.5540	1.6320	1.4187	1.2749	1.5031
W.A.T.	4.4276	7.6484	3.3050	3.7712	11.5666
Carcass	5.0894	5.6324	5.5069	3.1250	5.1167
Total body wt.	20.6320	25.7571	20.1716	18.5493	29.2404
Semilean body wt.	16.2044	18.1087	16.8666	14.7781	17.6738
Lean body wt.	15.3149	16.8486	15.6170	13.7959	16.4219

Table 4 (continued)

	Group B				
	51b	52b	53b	54b	55b
Skin	1.8381	1.9891	2.3634	1.9350	2.0379
Muscle ant. body	3.8749	3.7440	3.6903	3.8630	4.1504
Muscle post. body	1.4340	1.3087	1.4057	1.6093	1.5990
Total muscle	5.3089	5.0527	5.0960	5.4723	5.7494
Diaphragm	0.1203	0.1039	0.1046	0.1110	0.0826
Interscap. B.A.T.	0.5624	0.4656	0.2495	0.2732	0.5505
Other B.A.T.	0.5247	0.5568	0.2685	0.1769	0.4440
Total B.A.T.	1.0871	1.0224	0.5180	0.4501	0.9945
Liver	0.9942	0.6122	0.8524	0.8256	0.7226
Kidneys	0.2225	0.1631	0.2608	0.1962	0.2003
Stomach	0.1551	0.1455	0.1577	0.1430	0.1498
Intestine	0.7351	0.5118	0.8084	0.7849	0.4975
Myocardium	0.1662	0.1596	0.1701	0.1245	0.1377
Blood	1.2252	1.2554	1.5911	1.3847	1.7448
W.A.T.	7.2163	4.4488	3.8411	3.7350	6.2100
Carcass	5.5655	5.2227	5.4668	5.4034	6.1092
Total body wt.	24.6345	20.6872	21.2304	20.5657	24.6363
Semilean body wt.	17.4182	16.2384	17.3893	16.8307	18.4263
Lean body wt.	16.3311	15.2160	16.8713	16.3806	17.4318
	56b	57b	58b	59b	60b
Skin	1.8817	2.3130	1.5723	2.5099	1.8547
Muscle ant. body	3.5487	3.6055	3.4195	5.0273	4.4241
Muscle post. body	1.3752	1.4235	1.1837	1.6134	1.5260
Total muscle	4.9239	5.0290	4.6032	6.6407	5.9501
Diaphragm	0.1094	0.1198	0.0922	0.0975	0.1241
Interscap. B.A.T.	0.4870	0.5136	0.3763	0.3280	0.5379
Other B.A.T.	0.4580	0.4518	0.4595	0.3426	0.4955
Total B.A.T.	0.9450	0.9654	0.8358	0.6706	1.0334
Liver	0.6533	0.6630	0.5942	0.8635	0.8851
Kidneys	0.1390	0.1980	0.1627	0.1826	0.2081
Stomach	0.1216	0.1412	0.0982	0.2164	0.1582
Intestine	0.3766	0.6531	0.6262	0.6592	0.5646
Myocardium	0.1304	0.1595	0.1207	0.1503	0.1600
Blood	1.3595	1.3449	1.2910	1.3474	1.7330
W.A.T.	5.0508	11.1127	3.2164	2.3251	5.0780
Carcass	5.0980	5.0780	5.1051	5.9202	5.8087
Total body wt.	20.7892	27.7776	18.3180	21.5834	23.5580
Semilean body wt.	15.7384	16.6649	15.1016	19.2583	18.4800
Lean body wt.	14.7934	15.6995	14.2658	18.5877	17.4466

Table 4 (continued)

	Group B				
	61b	62b	63b	64b	65b
Skin	1.6746	2.6690	1.9931	1.7047	1.5459
Muscle ant. body	3.5783	5.2009	3.6687	3.9815	3.3042
Muscle post. body	1.2676	1.7462	1.4270	1.5009	1.2767
Total muscle	4.8459	6.9471	5.0957	5.4824	4.5809
Diaphragm	0.1243	0.1200	0.1217	0.1002	0.0995
Interscap. B.A.T.	0.4297	0.3177	0.5701	0.3755	0.4517
Other B.A.T.	0.3049	0.3163	0.6267	0.3304	0.3760
Total B.A.T.	0.7346	0.6340	1.1968	0.7059	0.8277
Liver	0.7363	0.8035	0.9830	0.7640	0.8466
Kidneys	0.1950	0.2066	0.1987	0.2110	0.2143
Stomach	0.1565	0.2080	0.1210	0.1766	0.1538
Intestine	0.8801	0.6237	0.5779	0.7325	0.7400
Myocardium	0.1426	0.1648	0.1713	0.1566	0.1387
Blood	1.4474	1.5633	1.4607	1.4423	1.4003
W.A.T.	2.2382	1.7235	4.6203	4.1556	2.8590
Carcass	5.5388	6.8110	5.6865	5.6718	5.4645
Total body wt.	18.7143	22.4745	22.2267	21.3036	18.8712
Semilean body wt.	16.4761	20.7510	17.6064	17.1480	16.0122
Lean body wt.	15.7415	20.1170	16.4096	16.4421	15.1845

	66b	67b	68b	69b	70b
Skin	2.0963	1.9501	2.1315	2.1938	1.9872
Muscle ant. body	5.0775	3.9997	3.7817	4.9787	3.9725
Muscle post. body	1.8338	1.5060	1.3707	1.7327	1.5166
Total muscle	6.9113	5.5057	5.1524	6.7114	5.4891
Diaphragm	0.1259	0.0980	0.0945	0.1620	0.1175
Interscap. B.A.T.	0.5342	0.4230	0.3481	0.4325	0.5300
Other B.A.T.	0.4996	0.4304	0.3125	0.3710	0.4516
Total B.A.T.	1.0338	0.8534	0.6606	0.8035	0.9816
Liver	0.6612	0.7562	0.6494	1.0932	0.8027
Kidneys	0.2376	0.2251	0.1938	0.3136	0.1763
Stomach	0.1682	0.1412	0.1137	0.2100	0.1610
Intestine	0.5369	0.3034	0.4597	0.9122	0.5718
Myocardium	0.1763	0.1235	0.1364	0.2124	0.1593
Blood	1.3518	1.4410	1.4440	1.5305	1.6190
W.A.T.	3.6771	1.5814	4.3083	7.2683	7.0168
Carcass	6.3538	5.4753	5.1486	6.4320	5.6915
Total body wt.	23.3302	18.4543	20.4929	27.8429	24.7738
Semilean body wt.	19.6531	16.8729	16.1846	20.5746	17.7570
Lean body wt.	18.6193	16.0195	15.5240	19.7711	16.7754

Table 4 (continued)

	Group B				
	71b	72b	73b	74b	75b
Skin	2.4434	1.8687	1.7336	1.7899	1.9878
Muscle ant. body	4.1449	3.9292	4.5012	3.2327	3.1877
Muscle post. body	1.4887	1.2430	1.6446	1.2338	1.2018
Total muscle	5.6336	5.1722	6.1458	4.4665	4.3895
Diaphragm	0.1032	0.1190	0.1110	0.1063	0.1013
Interscap. B.A.T.	0.5481	0.5434	0.8569	0.4620	0.5091
Other B.A.T.	0.4879	0.5702	0.6825	0.3682	0.4978
Total B.A.T.	1.0360	1.1136	1.5394	0.8302	1.0069
Liver	1.1143	0.6073	1.2612	0.6929	0.5339
Kidneys	0.1760	0.1382	0.2630	0.1392	0.1514
Stomach	0.1560	0.1068	0.1675	0.0743	0.1026
Intestine	0.5735	0.4750	0.7830	0.4622	0.5109
Myocardium	0.1512	0.1463	0.1650	0.1080	0.1328
Blood	1.3341	1.3256	1.4983	1.2164	1.2706
W.A.T.	5.7398	5.7503	3.2365	2.2030	6.3690
Carcass	5.7153	5.0638	6.1936	4.4436	5.1614
Total body wt.	24.1764	21.8868	23.0979	16.5325	21.7181
Semilean body wt.	18.4366	16.1365	19.8614	14.3295	15.3491
Lean body wt.	17.4006	15.0229	18.3220	13.4993	14.3422
	76b	77b	78b	79b	80b
Skin	1.9125	1.6554	1.6345	2.2078	1.8344
Muscle ant. body	3.6046	3.6217	3.8733	4.1407	4.5197
Muscle post. body	1.3036	1.4002	1.3089	1.5847	1.5199
Total muscle	4.9082	5.0219	5.1822	5.7254	6.0396
Diaphragm	0.1057	0.1005	0.1069	0.1206	0.1192
Interscap. B.A.T.	0.6490	0.3715	0.3976	0.3952	0.5392
Other B.A.T.	0.5574	0.3351	0.3931	0.3683	0.4206
Total B.A.T.	1.2064	0.7066	0.7907	0.7635	0.9598
Liver	0.5870	0.6184	0.5786	0.8830	1.0922
Kidneys	0.1373	0.1814	0.1604	0.1900	0.1849
Stomach	0.1023	0.1354	0.1230	0.1625	0.1494
Intestine	0.3868	0.4664	0.5932	0.5841	0.5976
Myocardium	0.1210	0.1445	0.1446	0.1448	0.1509
Blood	1.2690	1.4070	1.2836	1.2605	1.3447
W.A.T.	6.4677	5.3286	1.9373	5.6796	2.9028
Carcass	5.0355	4.8710	5.5278	5.9299	6.4662
Total body wt.	22.2394	20.6371	18.0628	23.6517	21.8417
Semilean body wt.	15.7717	15.3085	16.1255	17.9721	18.9389
Lean body wt.	14.5653	14.6019	15.3348	17.2086	17.9791

Table 4 (continued)

	Group B				
	81b	82b	83b	84b	85b
Skin	1.9313	2.3466	2.5020	1.6151	1.9560
Muscle ant. body	4.4944	4.2218	4.4410	3.9309	3.9574
Muscle post. body	1.6434	1.5951	1.6390	1.5300	1.4743
Total muscle	6.1378	5.8169	6.0800	5.4609	5.4317
Diaphragm	0.1360	0.1289	0.1349	0.1149	0.0971
Interscap. B.A.T.	0.3991	0.4880	0.4106	0.3695	0.5912
Other B.A.T.	0.3187	0.5292	0.3557	0.3605	0.5135
Total B.A.T.	0.7178	1.0172	0.7663	0.7000	1.1047
Liver	0.9148	0.6910	0.9229	0.7908	0.7136
Kidneys	0.2200	0.1555	0.2413	0.1758	0.1530
Stomach	0.2322	0.1096	0.1407	0.1717	0.1526
Intestine	0.9250	0.4814	0.6824	0.6713	0.4862
Myocardium	0.1500	0.1544	0.1566	0.1668	0.1510
Blood	1.4603	1.4203	1.4764	1.5227	1.0662
W.A.T.	6.9779	6.3811	4.8665	2.7600	4.7305
Carcass	6.4147	5.8045	5.9002	5.6470	4.7655
Total body wt.	26.2178	24.5074	23.8702	19.8270	20.8081
Semilean body wt.	19.2399	18.1263	19.0037	17.0670	16.0776
Lean body wt.	18.5221	17.1091	18.2374	16.3670	14.9729
	86b	87b	88b	89b	90b
Skin	1.4169	2.3329	1.5040	2.8300	1.6799
Muscle ant. body	3.8079	3.9855	2.9394	4.4290	4.2000
Muscle post. body	1.3044	1.6178	1.1912	1.7981	1.7889
Total muscle	5.1123	5.6033	4.1306	6.2271	5.9889
Diaphragm	0.1018	0.1116	0.1130	0.1350	0.1458
Interscap. B.A.T.	0.4885	0.4190	0.4774	0.6083	0.5057
Other B.A.T.	0.5417	0.3636	0.4191	0.4458	0.6198
Total B.A.T.	1.0302	0.7826	0.8965	1.0541	1.1255
Liver	0.7379	0.7057	0.7397	0.9555	0.9379
Kidneys	0.1638	0.2050	0.1583	0.1686	0.2092
Stomach	0.1624	0.1336	0.1197	0.1230	0.1448
Intestine	0.5518	0.5250	0.5934	0.4402	0.4540
Myocardium	0.1341	0.1385	0.1902	0.1438	0.1669
Blood	1.2639	1.7434	1.2187	1.7300	1.5514
W.A.T.	5.7770	7.2335	5.0663	15.4160	6.0880
Carcass	4.7267	5.5554	4.0476	5.8986	5.7107
Total body wt.	21.1788	25.0705	18.7780	35.1219	24.2030
Semilean body wt.	15.4018	17.8370	13.7117	19.7059	18.1150
Lean body wt.	14.3716	17.0544	12.8152	18.6518	16.9895

Table 4 (continued)

	Group B			
	91b	92b	93b	94b
Skin	2.5087	2.2901	1.9410	2.2769
Muscle ant. body	4.3192	5.3720	3.9472	3.8996
Muscle post. body	1.7315	1.7864	1.4305	1.5872
Total muscle	6.0507	7.1584	5.3777	5.4868
Diaphragm	0.1449	0.1297	0.1166	0.1510
Interscap. B.A.T.	0.3930	0.4667	0.4363	0.4482
Other B.A.T.	0.3405	0.4520	0.3907	0.4041
Total B.A.T.	0.7335	0.9187	0.8270	0.8523
Liver	0.8778	1.0441	0.9597	0.9836
Kidneys	0.2732	0.2767	0.1718	0.2002
Stomach	0.1420	0.1621	0.0949	0.1335
Intestine	0.5462	0.8191	0.4755	0.5415
Myocardium	0.1956	0.1614	0.1381	0.1449
Blood	1.7736	1.5568	1.2041	1.2993
W.A.T.	6.0147	7.0610	7.2116	5.2607
Carcass	6.1180	6.1968	5.5301	5.0610
Total body wt.	25.3789	27.7749	24.0481	22.3917
Semilean body wt.	19.3642	20.7139	16.8365	17.1310
Lean body wt.	18.6307	19.7952	16.0095	16.2787

	Mean	s_d (±)
Skin	1.9959	0.3595
Muscle ant. body	3.9645	0.4910
Muscle post. body	1.4717	0.1739
Total muscle	5.4362	0.6309
Diaphragm	0.1133	0.0159
Interscap. B.A.T.	0.4834	0.0993
Other B.A.T.	0.4507	0.0944
Total B.A.T.	0.9338	0.1820
Liver	0.7534	0.1621
Kidneys	0.1852	0.0383
Stomach	0.1396	0.0287
Intestine	0.5783	0.1284
Myocardium	0.1482	0.0213
Blood	1.4316	0.1724
W.A.T.	5.1042	2.2986
Carcass	5.4987	0.6051
Total body wt.	22.3188	3.2628
Semilean body wt.	17.2146	2.9252
Lean body wt.	16.2808	1.7012

Table 5. Organ and tissue weights (expressed as a percentage of semilean body weight) of *E. fuscus*, sacrificed at different heart rates during arousal from hibernation in the winter

	Group B				
	1b	2b	3b	4b	5b
Skin	10.94	9.87	11.12	10.41	10.00
Muscle ant. body	23.03	23.43	24.05	23.11	22.27
Muscle post. body	8.87	8.83	8.09	9.63	8.95
Total muscle	31.91	32.27	32.14	32.75	31.22
Diaphragm	0.57	0.60	0.60	0.65	0.62
Interscap. B.A.T.	2.55	2.94	3.23	2.64	3.40
Other B.A.T.	2.27	2.63	3.81	2.46	3.31
Total B.A.T.	4.82	5.57	7.04	5.10	6.71
Liver	4.76	4.57	4.27	4.02	3.59
Kidneys	1.10	0.97	0.85	0.76	0.99
Stomach	0.70	0.78	0.74	0.83	0.89
Intestine	3.09	4.30	3.46	4.08	3.77
Myocardium	0.78	0.75	0.75	0.80	1.00
Blood	8.34	8.32	8.47	8.46	8.71
Carcass	33.00	31.99	30.56	32.14	32.49
	6b	7b	8b	9b	10b
Skin	10.43	12.35	11.23	14.42	9.85
Muscle ant. body	22.55	22.01	22.39	22.39	23.84
Muscle post. body	8.79	8.69	7.86	8.58	8.28
Total muscle	31.34	30.70	30.24	30.97	32.12
Diaphragm	0.66	0.62	0.60	0.66	0.63
Interscap. B.A.T.	3.12	2.33	2.75	2.49	2.49
Other B.A.T.	2.62	2.43	2.37	2.22	2.47
Total B.A.T.	5.74	4.76	5.12	4.72	4.96
Liver	3.98	4.40	4.52	4.15	4.47
Kidneys	1.00	1.11	0.95	1.09	0.96
Stomach	1.10	0.64	0.72	1.00	0.76
Intestine	2.74	3.05	3.41	3.57	3.71
Myocardium	0.75	0.85	0.87	0.85	0.77
Blood	8.04	8.37	9.59	7.89	10.34
Carcass	34.25	33.15	32.74	30.67	31.43

Table 5 (continued)

	Group B				
	11b	12b	13b	14b	15b
Skin	9.31	10.33	10.88	10.07	11.68
Muscle ant. body	22.46	23.09	21.06	22.65	22.58
Muscle post. body	8.45	8.95	8.82	8.77	8.41
Total muscle	30.90	32.05	29.87	31.42	31.00
Diaphragm	0.56	0.56	0.65	0.73	0.66
Interscap. B.A.T.	3.40	3.45	2.91	3.13	2.33
Other B.A.T.	2.73	3.16	2.80	2.88	1.96
Total B.A.T.	6.13	6.61	5.71	6.01	4.28
Liver	3.81	4.57	3.97	3.48	4.80
Kidneys	1.03	0.74	1.13	1.17	1.12
Stomach	0.88	0.76	0.81	0.82	0.81
Intestine	3.03	2.44	3.69	3.55	3.75
Myocardium	0.90	0.81	0.94	0.82	0.84
Blood	8.41	8.38	9.56	9.21	9.70
Carcass	35.04	32.76	32.79	32.72	31.36
	16b	17b	18b	19b	20b
Skin	12.46	9.60	12.00	11.64	11.91
Muscle ant. body	22.70	22.31	20.57	23.33	22.87
Muscle post. body	7.46	8.81	8.97	8.07	8.71
Total muscle	30.16	31.12	29.54	31.40	31.58
Diaphragm	0.51	0.83	0.55	0.69	0.75
Interscap. B.A.T.	2.93	2.83	3.65	2.99	2.81
Other B.A.T.	2.88	2.81	3.25	2.97	2.51
Total B.A.T.	5.81	5.64	6.89	5.96	5.31
Liver	4.31	2.78	5.00	3.19	3.84
Kidneys	1.12	0.86	0.80	0.85	1.18
Stomach	0.84	0.84	0.88	0.93	0.72
Intestine	3.93	2.86	2.32	3.08	3.18
Myocardium	0.93	0.79	0.85	0.84	0.75
Blood	7.83	10.96	8.81	8.18	9.50
Carcass	32.08	33.71	32.34	33.25	31.27

Table 5 (continued)

	Group B				
	21b	22b	23b	24b	25b
Skin	14.30	12.19	11.15	11.70	10.78
Muscle ant. body	21.59	22.08	21.47	24.04	24.18
Muscle post. body	7.83	8.08	8.47	9.07	9.34
Total muscle	29.42	30.16	29.94	33.11	33.52
Diaphragm	0.69	0.58	0.63	0.74	0.64
Interscap. B.A.T.	2.57	3.08	1.81	2.57	3.64
Other B.A.T.	1.99	2.71	2.29	2.36	2.62
Total B.A.T.	4.56	5.79	4.10	4.93	6.27
Liver	5.18	4.03	5.20	3.27	4.23
Kidneys	1.02	1.03	1.33	1.11	0.76
Stomach	0.69	0.75	0.82	0.66	0.59
Intestine	3.20	2.84	3.57	3.05	3.07
Myocardium	0.91	0.81	0.96	0.89	0.78
Blood	9.67	9.05	8.56	7.57	7.45
Carcass	30.37	32.79	33.72	32.99	31.92
	26b	27b	28b	29b	30b
Skin	11.84	11.78	12.15	11.60	11.37
Muscle ant. body	22.31	22.51	22.52	22.09	22.68
Muscle post. body	8.30	8.24	7.45	8.08	8.49
Total muscle	30.61	30.75	29.97	30.17	31.17
Diaphragm	0.67	0.63	0.65	0.67	0.68
Interscap. B.A.T.	3.07	3.15	3.02	3.01	2.08
Other B.A.T.	3.12	3.26	3.12	2.82	2.47
Total B.A.T.	6.19	6.41	6.14	5.83	4.56
Liver	4.84	4.34	3.46	4.56	5.47
Kidneys	1.16	0.98	1.22	0.87	0.99
Stomach	0.75	0.71	0.75	0.74	0.83
Intestine	2.71	2.90	2.87	3.94	3.39
Myocardium	1.03	0.90	0.89	0.93	0.94
Blood	7.47	6.97	8.49	7.07	9.06
Carcass	32.74	33.63	33.42	33.63	31.54

Table 5 (continued)

	Group B				
	31b	32b	33b	34b	35b
Skin	12.44	11.61	12.93	16.95	10.90
Muscle ant. body	22.37	22.24	22.94	22.85	21.99
Muscle post. body	8.51	9.44	8.29	7.75	7.79
Total muscle	30.89	31.68	31.23	30.60	29.79
Diaphragm	0.68	0.65	0.63	0.54	0.63
Interscap. B.A.T.	2.28	2.93	2.77	1.65	2.68
Other B.A.T.	2.32	3.30	3.20	1.40	2.90
Total B.A.T.	4.60	6.23	5.98	3.05	5.58
Liver	4.08	3.87	2.87	3.34	3.80
Kidneys	1.00	0.86	0.94	1.10	1.21
Stomach	0.96	1.09	0.60	0.68	0.76
Intestine	3.98	2.95	3.16	3.90	4.73
Myocardium	0.88	1.09	0.79	0.76	0.97
Blood	8.06	8.77	7.20	8.16	8.70
Carcass	32.44	31.19	33.68	30.93	32.94
	36b	37b	38b	39b	40b
Skin	12.84	12.92	12.83	12.18	10.11
Muscle ant. body	22.84	22.98	22.81	23.05	22.02
Muscle post. body	8.35	8.13	8.07	9.76	9.24
Total muscle	31.19	31.11	30.88	32.81	31.26
Diaphragm	0.68	0.66	0.65	0.64	0.68
Interscap. B.A.T.	3.14	3.10	2.77	3.05	3.34
Other B.A.T.	2.63	2.58	2.45	2.50	3.42
Total B.A.T.	5.77	5.68	5.22	5.55	6.76
Liver	3.88	3.97	3.79	3.38	4.26
Kidneys	0.87	1.06	1.79	0.98	1.04
Stomach	0.83	0.85	0.76	0.55	0.85
Intestine	3.65	3.94	2.27	2.70	2.94
Myocardium	0.74	0.79	0.73	0.90	0.85
Blood	7.35	7.58	8.72	8.13	8.65
Carcass	32.20	31.44	32.34	32.19	32.60

Table 5 (continued)

	Group B				
	51b	52b	53b	54b	55b
Skin	10.55	12.25	13.59	11.50	11.06
Muscle ant. body	22.25	23.06	21.22	22.95	22.52
Muscle post. body	8.23	8.06	8.08	9.56	8.68
Total muscle	30.48	31.12	29.31	32.51	31.20
Diaphragm	0.69	0.64	0.60	0.66	0.45
Interscap. B.A.T.	3.23	2.87	1.43	1.62	2.99
Other B.A.T.	3.01	3.43	1.54	1.05	2.41
Total B.A.T.	6.24	6.30	2.98	2.67	5.40
Liver	5.71	3.77	4.90	4.91	3.92
Kidneys	1.28	1.00	1.50	1.17	1.09
Stomach	0.89	0.90	0.91	0.85	0.81
Intestine	4.22	3.15	4.65	4.66	2.70
Myocardium	0.95	0.98	0.98	0.74	0.75
Blood	7.03	7.73	9.15	8.23	9.47
Carcass	31.95	32.16	31.44	32.10	33.15
	56b	57b	58b	59b	60b
Skin	11.96	13.88	10.41	13.03	10.04
Muscle ant. body	22.55	21.64	22.64	26.10	23.94
Muscle post. body	8.74	8.54	7.84	8.38	8.26
Total muscle	31.29	30.18	30.48	34.48	32.20
Diaphragm	0.70	0.72	0.61	0.51	0.67
Interscap. B.A.T.	3.09	3.08	2.49	1.70	2.91
Other B.A.T.	2.91	2.71	3.04	1.78	2.68
Total B.A.T.	6.00	5.79	5.53	3.48	5.59
Liver	4.15	3.98	3.93	4.48	4.79
Kidneys	0.88	1.19	1.08	0.95	1.13
Stomach	0.77	0.85	0.65	1.12	0.86
Intestine	2.39	3.92	4.15	3.42	3.06
Myocardium	0.83	0.96	0.80	0.78	0.87
Blood	8.64	8.07	8.55	7.00	9.38
Carcass	32.39	30.47	33.81	30.74	31.43

Table 5 (continued)

	Group B				
	61b	62b	63b	64b	65b
Skin	10.16	12.86	11.32	9.94	9.65
Muscle ant. body	21.72	25.06	20.84	23.22	20.64
Muscle post. body	7.69	8.42	8.11	8.75	7.97
Total muscle	29.41	33.48	28.94	31.97	28.61
Diaphragm	0.75	0.58	0.69	0.58	0.62
Interscap. B.A.T.	2.61	1.53	3.24	2.19	2.82
Other B.A.T.	1.85	1.52	3.56	1.93	2.35
Total B.A.T.	4.46	3.06	6.80	4.12	5.17
Liver	4.47	3.87	5.58	4.46	5.29
Kidneys	1.18	1.00	1.13	1.23	1.34
Stomach	0.95	1.00	0.69	1.03	0.96
Intestine	5.34	3.01	3.28	4.27	4.62
Myocardium	0.87	0.79	0.97	0.91	0.87
Blood	8.78	7.53	8.30	8.41	8.75
Carcass	33.62	32.82	32.30	33.08	34.13
	66b	67b	68b	69b	70b
Skin	10.67	11.56	13.17	10.66	11.19
Muscle ant. body	25.84	23.70	23.37	24.20	22.37
Muscle post. body	9.33	8.93	8.47	8.42	8.54
Total muscle	35.17	32.63	31.84	32.62	30.91
Diaphragm	0.64	0.58	0.58	0.79	0.66
Interscap. B.A.T.	2.72	2.51	2.15	2.10	2.98
Other B.A.T.	2.54	2.55	1.93	1.80	2.54
Total B.A.T.	5.26	5.06	4.08	3.91	5.53
Liver	3.36	4.48	4.01	5.31	4.52
Kidneys	1.21	1.33	1.20	1.52	0.99
Stomach	0.86	0.84	0.70	1.02	0.91
Intestine	2.73	1.80	2.84	4.43	3.22
Myocardium	0.90	0.73	0.84	1.03	0.90
Blood	6.88	8.54	8.92	7.44	9.12
Carcass	32.33	32.45	31.81	31.26	32.05

Table 5 (continued)

	Group B				
	71b	72b	73b	74b	75b
Skin	13.25	11.58	8.73	12.49	12.95
Muscle ant. body	22.48	24.35	22.66	22.56	20.77
Muscle post. body	8.07	7.70	8.28	8.61	7.83
Total muscle	30.56	32.05	30.94	31.17	28.60
Diaphragm	0.56	0.74	0.56	0.74	0.66
Interscap. B.A.T.	2.97	3.37	4.31	3.22	3.32
Other B.A.T.	2.65	3.53	3.44	2.57	3.24
Total B.A.T.	5.62	6.90	7.75	5.79	6.56
Liver	6.04	3.76	6.35	4.84	3.48
Kidneys	0.95	0.86	1.32	0.97	0.99
Stomach	0.85	0.66	0.84	0.52	0.67
Intestine	3.11	2.94	3.94	3.23	3.33
Myocardium	0.82	0.91	0.83	0.75	0.87
Blood	7.24	8.21	7.54	8.49	8.28
Carcass	31.00	31.38	31.18	31.01	33.63
	76b	77b	78b	79b	80b
Skin	12.13	10.81	10.14	12.28	9.69
Muscle ant. body	22.85	23.66	24.02	23.04	23.86
Muscle post. body	8.27	9.15	8.12	8.82	8.03
Total muscle	31.12	32.80	32.14	31.86	31.89
Diaphragm	0.67	0.66	0.66	0.67	0.63
Interscap.B.A.T.	4.11	2.43	2.47	2.20	2.85
Other B.A.T.	3.53	2.19	2.44	2.05	2.22
Total B.A.T.	7.65	4.62	4.90	4.25	5.07
Liver	3.72	4.04	3.59	4.91	5.77
Kidneys	0.87	1.18	0.99	1.06	0.98
Stomach	0.65	0.88	0.76	0.90	0.79
Intestine	2.45	3.05	3.68	3.25	3.16
Myocardium	0.77	0.94	0.90	0.81	0.80
Blood	8.05	9.19	7.96	7.01	7.10
Carcass	31.93	31.82	34.28	33.00	34.14

Table 5 (continued)

	Group B				
	81b	82b	83b	84b	85b
Skin	10.04	12.95	13.17	9.46	12.17
Muscle ant. body	23.36	23.29	23.37	23.03	24.61
Muscle post. body	8.54	8.80	8.62	8.96	9.17
Total muscle	31.90	32.09	31.99	32.00	33.78
Diaphragm	0.71	0.71	0.71	0.67	0.60
Interscap. B.A.T.	2.07	2.69	2.16	2.16	3.68
Other B.A.T.	1.66	2.92	1.87	2.11	3.19
Total B.A.T.	3.73	5.61	4.03	4.10	6.87
Liver	4.75	3.81	4.86	4.63	4.44
Kidneys	1.14	0.86	1.27	1.03	0.95
Stomach	1.21	0.60	0.74	1.01	0.95
Intestine	4.81	2.66	3.59	3.93	3.02
Myocardium	0.78	0.85	0.82	0.98	0.94
Blood	7.59	7.84	7.77	8.92	6.63
Carcass	33.34	32.02	31.05	33.09	29.64
	86b	87b	88b	89b	90b
Skin	9.20	13.08	10.97	14.36	9.27
Muscle ant. body	24.72	22.34	21.44	22.48	23.19
Muscle post. body	8.47	9.07	8.69	9.12	9.88
Total muscle	33.19	31.41	30.12	31.60	33.06
Diaphragm	0.66	0.63	0.82	0.69	0.80
Interscap. B.A.T.	3.17	2.35	3.48	3.09	2.79
Other B.A.T.	3.52	2.04	3.06	2.26	3.42
Total B.A.T.	6.69	4.39	6.54	5.35	6.21
Liver	4.79	3.96	5.39	4.85	5.18
Kidneys	1.06	1.15	1.15	0.86	1.15
Stomach	1.05	0.75	0.87	0.62	0.80
Intestine	3.58	2.94	4.33	2.23	2.51
Myocardium	0.87	0.78	1.39	0.73	0.92
Blood	8.21	9.77	8.89	8.78	8.56
Carcass	30.69	31.15	29.52	29.93	31.52

Table 5 (continued)

	Group B			
	91b	92b	93b	94b
Skin	12.96	11.06	11.53	12.35
Muscle ant. body	22.31	25.93	23.44	21.15
Muscle post. body	8.94	8.62	8.50	8.61
Total muscle	31.25	34.56	31.94	29.76
Diaphragm	0.75	0.63	0.69	0.82
Interscap. B.A.T.	2.03	2.25	2.59	2.43
Other B.A.T.	1.76	2.18	2.32	2.19
Total B.A.T.	3.79	4.44	4.91	4.62
Liver	4.53	5.04	5.70	5.34
Kidneys	1.41	1.34	1.02	1.09
Stomach	0.73	0.78	0.56	0.72
Intestine	2.82	3.95	2.82	2.94
Myocardium	1.01	0.78	0.82	7.86
Blood	9.16	7.52	7.15	7.05
Carcass	31.59	29.92	32.85	27.45

	Mean	s_d (±)
Skin	11.55	1.43
Muscle ant. body	23.01	1.66
Muscle post. body	8.54	0.51
Total muscle	31.55	1.74
Diaphragm	0.65	0.07
Interscap. B.A.T.	2.82	0.57
Other B.A.T.	2.64	0.59
Total B.A.T.	5.46	1.10
Liver	4.35	0.70
Kidneys	1.07	0.17
Stomach	0.81	0.13
Intestine	3.36	0.66
Myocardium	0.94	0.72
Blood	8.33	0.84
Carcass	31.92	1.73

Table 6. Organ and tissue weights (expressed as a percentage of lean body weight) of *E. fuscus*, sacrificed at different heart rates during arousal from hibernation in the winter

	Group B				
	1b	2b	3b	4b	5b
Skin	11.50	10.46	11.96	10.97	10.72
Muscle ant. body	24.20	24.82	25.87	24.36	23.88
Muscle post. body	9.32	9.36	8.70	10.15	9.60
Total muscle	33.52	34.17	34.58	34.51	33.47
Diaphragm	0.59	0.64	0.65	0.68	0.66
Liver	5.00	4.84	4.60	4.23	3.84
Kidneys	1.16	1.03	0.91	0.80	1.07
Stomach	0.73	0.82	0.79	0.87	0.95
Intestine	3.25	4.55	3.72	4.30	4.04
Myocardium	0.82	0.79	0.80	0.85	1.07
Blood	8.76	8.81	9.11	8.91	9.34
Carcass	34.68	33.88	32.88	33.86	34.83
	6b	7b	8b	9b	10b
Skin	11.06	12.97	11.84	15.13	10.36
Muscle ant. body	23.92	23.11	23.60	23.50	25.08
Muscle post. body	9.33	9.12	8.28	9.01	8.71
Total muscle	33.25	32.23	31.88	32.50	33.79
Diaphragm	0.70	0.65	0.63	0.70	0.67
Liver	4.22	4.62	4.77	4.35	4.71
Kidneys	1.06	1.17	1.00	1.15	1.01
Stomach	1.16	0.67	0.76	1.05	0.80
Intestine	2.90	3.20	3.59	3.75	3.90
Myocardium	0.80	0.89	0.92	0.89	0.81
Blood	8.53	8.79	10.10	8.28	10.88
Carcass	36.33	34.80	34.51	32.19	33.07

Table 6 (continued)

	Group B				
	11b	12b	13b	14b	15b
Skin	9.92	11.06	11.54	10.72	12.21
Muscle ant. body	23.93	24.73	22.33	24.10	23.59
Muscle post. body	9.00	9.59	9.35	9.33	8.79
Total muscle	32.93	34.31	31.68	33.43	32.39
Diaphragm	0.59	0.60	0.69	0.77	0.69
Liver	4.06	4.89	4.21	3.70	5.02
Kidneys	1.10	0.80	1.20	1.24	1.17
Stomach	0.94	0.82	0.86	0.88	0.84
Intestine	3.23	2.61	3.91	3.78	3.92
Myocardium	0.94	0.87	1.00	0.87	0.88
Blood	8.96	8.97	10.14	9.80	10.13
Carcass	37.34	35.08	34.77	34.82	32.77
	16b	17b	18b	19b	20b
Skin	13.23	10.17	12.89	12.38	12.58
Muscle ant. body	24.10	23.64	22.10	24.81	24.16
Muscle post. body	7.92	9.34	9.63	8.58	9.20
Total muscle	32.03	32.98	31.73	33.39	33.36
Diaphragm	0.54	0.88	0.59	0.74	0.79
Liver	4.58	2.95	5.38	3.39	4.06
Kidneys	1.19	0.91	0.86	0.90	1.25
Stomach	0.90	0.89	0.94	0.99	0.76
Intestine	4.18	3.04	2.49	3.27	3.36
Myocardium	0.99	0.83	0.92	0.89	0.79
Blood	8.32	11.62	9.47	8.70	10.03
Carcass	34.06	35.73	34.73	35.35	33.03

Table 6 (continued)

	Group B				
	21b	22b	23b	24b	25b
Skin	14.98	12.94	11.63	12.31	11.50
Muscle ant. body	22.63	23.43	22.39	25.28	25.79
Muscle post. body	8.20	8.57	8.84	9.54	9.97
Total muscle	30.83	32.01	31.22	34.82	35.76
Diaphragm	0.72	0.62	0.66	0.78	0.68
Liver	5.43	4.27	5.42	3.44	4.51
Kidneys	1.07	1.09	1.39	1.16	0.81
Stomach	0.72	0.79	0.86	0.69	0.63
Intestine	3.35	3.01	3.72	3.21	3.27
Myocardium	0.95	0.85	1.00	0.93	0.83
Blood	10.13	9.60	8.93	7.96	7.95
Carcass	31.82	34.80	35.16	34.70	34.05
	26b	27b	28b	29b	30b
Skin	12.62	12.58	12.94	12.32	11.91
Muscle ant. body	23.78	24.06	24.00	23.46	23.77
Muscle post. body	8.85	8.80	7.94	8.58	8.89
Total muscle	32.63	32.86	31.93	32.03	32.66
Diaphragm	0.71	0.68	0.69	0.71	0.72
Liver	5.16	4.63	3.68	4.85	5.73
Kidneys	1.24	1.05	1.30	0.93	1.04
Stomach	0.80	0.76	0.80	0.79	0.87
Intestine	2.89	3.09	3.06	4.18	3.55
Myocardium	1.10	0.96	0.95	0.99	0.99
Blood	7.96	7.45	9.05	7.50	9.49
Carcass	34.90	35.94	35.61	35.71	33.05

Table 6 (continued)

	Group B				
	31b	32b	33b	34b	35b
Skin	13.04	12.38	13.75	17.48	11.54
Muscle ant. body	23.45	23.72	24.40	23.57	23.29
Muscle post. body	8.93	10.07	8.81	7.99	8.26
Total muscle	32.38	33.79	33.22	31.56	31.55
Diaphragm	0.71	0.69	0.67	0.55	0.67
Liver	4.28	4.13	3.05	3.45	4.02
Kidneys	1.05	0.91	1.00	1.13	1.28
Stomach	1.01	1.17	0.63	0.70	0.80
Intestine	4.17	3.15	3.36	4.03	5.01
Myocardium	0.92	1.17	0.84	0.78	1.03
Blood	8.44	9.36	7.66	8.42	9.21
Carcass	34.00	33.26	35.82	31.90	34.88
	36b	37b	38b	39b	40b
Skin	13.63	13.69	13.54	12.90	10.85
Muscle ant. body	24.24	24.36	24.06	24.40	23.62
Muscle post. body	8.86	8.62	8.52	10.33	9.91
Total muscle	33.10	32.99	32.58	34.74	33.53
Diaphragm	0.72	0.70	0.69	0.67	0.73
Liver	4.12	4.21	4.00	3.58	4.57
Kidneys	0.93	1.13	1.89	1.03	1.12
Stomach	0.88	0.90	0.81	0.58	0.91
Intestine	3.88	4.17	2.40	2.86	3.15
Myocardium	0.78	0.83	0.77	0.95	0.92
Blood	7.80	8.04	9.21	8.60	9.28
Carcass	34.17	33.34	34.12	34.08	34.96

Table 6 (continued)

	Group B				
	41b	42b	43b	44b	45b
Skin	12.22	13.93	11.76	12.24	15.13
Muscle ant. body	24.29	24.85	24.90	27.50	24.77
Muscle post. body	9.03	9.12	9.46	9.42	9.80
Total muscle	33.32	33.97	34.36	36.92	34.57
Diaphragm	0.84	0.70	0.73	0.68	0.85
Liver	3.85	4.88	3.59	3.79	4.29
Kidneys	1.02	1.30	0.89	0.90	1.18
Stomach	0.92	0.74	0.84	0.74	0.74
Intestine	3.58	3.12	2.99	2.95	3.66
Myocardium	0.75	0.79	1.04	0.92	0.96
Blood	9.36	8.87	8.69	8.68	7.52
Carcass	34.14	31.71	35.12	32.18	31.10
	46b	47b	48b	49b	50b
Skin	10.12	12.00	10.91	10.74	13.60
Muscle ant. body	25.37	24.57	21.98	37.16	24.60
Muscle post. body	9.63	9.18	8.84	8.25	9.17
Total muscle	35.00	33.76	30.82	45.41	33.78
Diaphragm	0.79	0.81	0.69	0.68	0.73
Liver	4.10	4.48	5.39	4.68	4.86
Kidneys	1.00	1.38	1.29	1.30	1.09
Stomach	0.93	0.82	1.19	0.99	0.62
Intestine	3.82	2.71	4.38	3.46	4.07
Myocardium	0.87	0.93	0.99	0.84	0.94
Blood	10.15	9.69	9.08	9.24	9.15
Carcass	33.23	33.43	35.26	22.65	31.16

Table 6 (continued)

	Group B				
	51b	52b	53b	54b	55b
Skin	11.26	13.07	14.01	11.81	11.69
Muscle ant. body	23.73	24.61	21.87	23.58	23.81
Muscle post. body	8.78	8.60	8.33	9.82	9.17
Total muscle	32.51	33.21	30.21	33.41	32.98
Diaphragm	0.74	0.68	0.62	0.68	0.47
Liver	6.09	4.02	5.05	5.04	4.15
Kidneys	1.36	1.07	1.55	1.20	1.15
Stomach	0.95	0.96	0.93	0.87	0.86
Intestine	4.50	3.36	4.79	4.79	2.85
Myocardium	1.02	1.05	1.01	0.76	0.79
Blood	7.50	8.25	9.43	8.45	10.01
Carcass	34.08	34.32	32.40	32.99	35.05
	56b	57b	58b	59b	60b
Skin	12.72	14.73	11.02	13.50	10.63
Muscle ant. body	23.99	22.97	23.97	27.05	25.36
Muscle post. body	9.30	9.07	8.30	8.68	8.75
Total muscle	33.28	32.03	32.27	35.73	34.10
Diaphragm	0.74	0.76	0.65	0.52	0.71
Liver	4.42	4.22	4.17	4.65	5.07
Kidneys	0.94	1.26	1.14	0.98	1.19
Stomach	0.82	0.90	0.69	1.16	0.91
Intestine	2.55	4.16	4.39	3.55	3.24
Myocardium	0.88	1.02	0.85	0.81	0.92
Blood	9.19	8.57	9.05	7.25	9.93
Carcass	34.46	32.34	35.79	31.85	33.29

Table 6 (continued)

	Group B				
	61b	62b	63b	64b	65b
Skin	10.64	13.27	12.15	10.37	10.18
Muscle ant. body	22.73	25.85	22.36	24.22	21.76
Muscle post. body	8.05	8.68	8.70	9.13	8.41
Total muscle	30.78	34.53	31.05	33.34	30.17
Diaphragm	0.79	0.60	0.74	0.61	0.66
Liver	4.68	3.99	5.99	4.65	5.58
Kidneys	1.24	1.03	1.21	1.28	1.41
Stomach	0.99	1.03	0.74	1.07	1.01
Intestine	5.59	3.10	3.52	4.46	4.87
Myocardium	0.91	0.82	1.04	0.95	0.91
Blood	9.19	7.77	8.90	8.77	9.22
Carcass	35.19	33.86	34.65	34.50	35.99
	66b	67b	68b	69b	70b
Skin	11.26	12.17	13.73	11.10	11.85
Muscle ant. body	27.27	24.97	24.36	25.18	23.68
Muscle post. body	9.85	9.40	8.83	8.76	9.04
Total muscle	37.12	34.37	33.19	33.95	32.72
Diaphragm	0.68	0.61	0.61	0.82	0.70
Liver	3.55	4.72	4.18	5.53	4.78
Kidneys	1.28	1.41	1.25	1.59	1.05
Stomach	0.90	0.88	0.73	1.06	0.96
Intestine	2.88	1.89	2.96	4.61	3.41
Myocardium	0.95	0.77	0.88	1.07	0.95
Blood	7.26	9.00	9.30	7.74	9.65
Carcass	34.12	34.18	33.17	32.53	33.93

Table 6 (continued)

	Group B				
	71b	72b	73b	74b	75b
Skin	14.04	12.44	9.46	13.26	13.86
Muscle ant. body	23.82	26.15	24.57	23.95	22.23
Muscle post. body	8.56	8.27	8.98	9.14	8.38
Total muscle	32.38	34.43	33.54	33.09	30.61
Diaphragm	0.59	0.79	0.61	0.79	0.71
Liver	6.40	4.04	6.88	5.13	3.72
Kidneys	1.01	0.92	1.44	1.03	1.06
Stomach	0.90	0.71	0.91	0.55	0.72
Intestine	3.30	3.16	4.27	3.42	3.56
Myocardium	0.87	0.97	0.90	0.80	0.93
Blood	7.67	8.82	8.18	9.01	8.86
Carcass	32.85	33.71	33.80	32.92	35.99
	76b	77b	78b	79b	80b
Skin	13.13	11.34	10.66	12.83	10.20
Muscle ant. body	24.75	24.80	25.26	24.06	25.14
Muscle post. body	8.95	9.59	8.54	9.21	8.45
Total muscle	33.70	34.39	33.79	33.27	33.59
Diaphragm	0.73	0.69	0.70	0.70	0.66
Liver	4.03	4.24	3.77	5.13	6.07
Kidneys	0.94	1.24	1.05	1.10	1.03
Stomach	0.70	0.93	0.80	0.94	0.83
Intestine	2.66	3.19	3.87	3.39	3.32
Myocardium	0.83	0.99	0.94	0.84	0.84
Blood	8.71	9.64	8.37	7.32	7.48
Carcass	34.57	33.36	36.05	34.46	35.97

Table 6 (continued)

	Group B			
	91b	92b	93b	94b
Skin	13.47	11.57	12.12	13.99
Muscle ant. body	23.18	27.14	24.66	23.96
Muscle post. body	9.29	9.02	8.94	9.75
Total muscle	32.48	36.16	33.59	33.71
Diaphragm	0.78	0.66	0.73	0.93
Liver	4.71	5.27	5.99	6.04
Kidneys	1.47	1.40	1.07	1.23
Stomach	0.76	0.82	0.59	0.82
Intestine	2.93	4.14	2.97	3.33
Myocardium	1.05	0.82	0.86	0.89
Blood	9.52	7.86	7.52	7.98
Carcass	32.84	31.30	34.54	31.09

	Mean	s_d (±)
Skin	12.23	1.48
Muscle ant. body	24.36	1.76
Muscle post. body	9.04	0.54
Total muscle	33.40	1.86
Diaphragm	0.70	0.07
Liver	4.61	0.75
Kidneys	1.13	0.18
Stomach	0.86	0.14
Intestine	3.55	0.68
Myocardium	0.91	0.10
Blood	8.82	0.87
Carcass	33.79	1.79

Table 7. Organ, tissue, and body weights (grams) of *E. fuscus*, sacrificed at different heart rates during arousal from hibernation in the summer

	Group C				
	1c	2c	3c	4c	5c
Skin	1.4781	1.8924	1.5026	2.3788	1.7536
Muscle ant. body	3.9600	4.2207	3.4270	3.7126	3.8509
Muscle post. body	1.3410	1.2794	1.2215	1.4481	1.4136
Total muscle	5.3010	5.5001	4.6485	5.1607	5.2645
Diaphragm	0.1027	0.1060	0.0947	0.0881	0.1013
Interscap. B.A.T.	0.2153	0.2442	0.2629	0.2311	0.2404
Other B.A.T.	0.2373	0.2354	0.2301	0.2463	0.2124
Total B.A.T.	0.4526	0.4796	0.4930	0.4774	0.4528
Liver	0.6556	0.7567	0.7160	0.6912	0.6587
Kidneys	0.1805	0.2474	0.2306	0.1906	0.1612
Stomach	0.1156	0.1627	0.1450	0.1832	0.1430
Intestine	0.5695	0.6263	0.6436	0.8941	0.4075
Myocardium	0.1128	0.1014	0.1078	0.1334	0.1403
Blood	1.1288	1.1463	1.1309	1.1334	1.1114
W.A.T.	0.0922	0.0696	0.4956	1.4184	0.5358
Carcass	4.7790	5.1400	4.7601	5.4245	4.9827
Total body wt.	14.9684	16.2285	14.9684	18.1738	15.7128
Semilean body wt.	14.8762	16.1589	14.4728	16.7554	15.1770
Lean body wt.	14.4236	15.6793	13.9798	16.2780	14.7242

	6c	7c	8c	9c	10c
Skin	1.7101	2.4269	1.2127	1.3962	1.9046
Muscle ant. body	4.0862	3.9594	3.6776	3.4577	3.9883
Muscle post. body	1.5483	1.3318	1.1262	1.2476	1.5031
Total muscle	5.6345	5.2912	4.8038	4.7053	5.4914
Diaphragm	0.1033	0.1026	0.0728	0.0914	0.1143
Interscap. B.A.T.	0.1640	0.2200	0.2123	0.1621	0.1794
Other B.A.T.	0.1545	0.1921	0.2159	0.1498	0.1756
Total B.A.T.	0.3185	0.4121	0.4282	0.3119	0.3550
Liver	0.5980	0.5784	0.5934	0.5870	0.8600
Kidneys	0.2875	0.1767	0.1547	0.1605	0.2222
Stomach	0.1602	0.1422	0.1394	0.1080	0.1810
Intestine	0.8357	0.4530	0.5890	0.6096	0.4717
Myocardium	0.1253	0.1500	0.1101	0.1042	0.1430
Blood	1.2053	1.0421	1.2312	1.1955	0.9607
W.A.T.	0.2720	0.8840	0.0000	0.8557	0.7402
Carcass	5.5067	5.6231	4.5030	5.2018	5.7888
Total body wt.	16.7571	17.2823	13.8383	15.3271	17.2329
Semilean body wt.	16.4851	16.3983	13.8383	14.4714	16.4927
Lean body wt.	16.1666	15.9862	13.4101	14.1595	16.1377

Table 7 (continued)

	Group C				
	11c	12c	13c	14c	15c
Skin	1.7456	1.5553	1.2930	1.4463	1.7053
Muscle ant. body	4.8753	4.4827	3.2535	3.5172	3.4633
Muscle post. body	1.7647	1.6118	1.1596	1.2346	1.2088
Total muscle	6.6400	6.0945	4.4131	4.7518	4.6721
Diaphragm	0.1212	0.1028	0.0714	0.0821	0.0721
Interscap. B.A.T.	0.1090	0.1612	0.1455	0.1890	0.1703
Other B.A.T.	0.2471	0.1642	0.1439	0.1783	0.1658
Total B.A.T.	0.3561	0.3254	0.2894	0.3673	0.3361
Liver	0.6138	0.5976	0.4709	0.6604	0.5735
Kidneys	0.2003	0.2246	0.1744	0.1570	0.1552
Stomach	0.1665	0.1373	0.1067	0.1414	0.0871
Intestine	0.4808	0.4401	0.4464	0.3909	0.4569
Myocardium	0.1305	0.1484	0.1060	0.1217	0.1120
Blood	1.1817	1.2542	1.1343	1.0366	0.9162
W.A.T.	0.6760	0.7691	0.3751	1.1591	0.4759
Carcass	5.6134	5.5854	4.5213	4.7127	4.5393
Total body wt.	17.9259	17.2347	13.4020	15.0273	14.1017
Semilean body wt.	17.2499	16.4656	13.0269	13.8682	13.6258
Lean body wt.	16.8938	16.1402	12.7375	13.5009	13.2897
	16c	17c	18c	19c	20c
Skin	1.8684	1.7820	1.9182	1.3803	1.8577
Muscle ant. body	3.4298	3.6480	3.2826	3.6769	4.0851
Muscle post. body	1.3089	1.3027	1.2339	1.2955	1.5170
Total muscle	4.7387	4.9507	4.5165	4.9724	5.6021
Diaphragm	0.0831	0.0869	0.0833	0.0778	0.0994
Interscap. B.A.T.	0.1757	0.1442	0.1724	0.2197	0.1953
Other B.A.T.	0.2048	0.1483	0.1633	0.2224	0.2141
Total B.A.T.	0.3805	0.2925	0.3357	0.4421	0.4094
Liver	0.8300	0.7606	0.5952	0.5826	0.7460
Kidneys	0.1637	0.1726	0.1799	0.1905	0.2013
Stomach	0.1185	0.1366	0.1028	0.1169	0.1331
Intestine	0.5597	0.6360	0.6967	0.4742	0.5931
Myocardium	0.1205	0.1508	0.1271	0.1201	0.1140
Blood	1.2452	1.1413	1.0516	1.0870	1.3330
W.A.T.	0.4612	0.6271	0.6276	0.8787	0.2482
Carcass	5.1302	5.0342	4.5994	4.8201	6.1292
Total body wt.	15.6997	15.7713	14.8340	15.1427	17.4665
Semilean body wt.	15.2385	15.1442	14.2064	14.2640	17.2183
Lean body wt.	14.8580	14.8517	13.8707	13.8219	16.8089

Table 7 (continued)

	Group C				
	21c	22c	23c	24c	25c
Skin	1.5830	2.1306	1.0439	1.2199	1.1144
Muscle ant. body	2.9355	4.4621	2.6932	3.3414	3.2487
Muscle post. body	1.1400	1.3815	1.0386	1.1860	1.2003
Total muscle	4.0755	5.8436	3.7318	4.5274	4.4490
Diaphragm	0.0957	0.1106	0.0803	0.1033	0.0951
Interscap. B.A.T.	0.7079	0.4308	0.1843	0.2900	0.2997
Other B.A.T.	0.6020	0.3475	0.1825	0.3044	0.2983
Total B.A.T.	1.3099	0.7783	0.3668	0.5944	0.5980
Liver	0.7058	0.6007	0.7655	0.5093	0.5013
Kidneys	0.1837	0.1543	0.1808	0.1471	0.1361
Stomach	0.1340	0.1408	0.1368	0.1670	0.1631
Intestine	0.6094	0.5020	0.5765	0.4467	0.4280
Myocardium	0.1298	0.1460	0.1196	0.1369	0.1351
Blood	1.0513	1.1580	1.0927	1.0369	1.1423
W.A.T.	2.2188	0.9572	0.1008	1.7692	1.2573
Carcass	4.4178	5.3269	4.4798	4.6794	4.7064
Total body wt.	16.5147	17.8490	12.6753	15.3375	14.7261
Semilean body wt.	14.2959	16.8918	12.5745	13.5683	13.4688
Lean body wt.	12.9860	16.1135	12.2077	12.9739	12.8708
	26c	27c	28c	29c	30c
Skin	1.4930	1.3793	1.8095	1.4629	1.8503
Muscle ant. body	3.9308	3.1693	3.1099	3.6425	4.2939
Muscle post. body	1.2822	1.1580	1.3613	1.2496	1.5754
Total muscle	5.2130	4.3273	4.4712	4.8921	5.8693
Diaphragm	0.0854	0.0765	0.0910	0.0980	0.1002
Interscap. B.A.T.	0.2046	0.1740	0.6129	0.3506	0.3887
Other B.A.T.	0.1929	0.1731	0.6326	0.3706	0.4007
Total B.A.T.	0.3975	0.3471	1.2455	0.7212	0.7894
Liver	0.6067	0.5374	0.6779	0.7227	0.7787
Kidneys	0.1532	0.1742	0.1615	0.1559	0.1500
Stomach	0.1577	0.1250	0.2158	0.1539	0.1713
Intestine	0.3665	0.5940	0.4681	0.4848	0.4080
Myocardium	0.1236	0.1354	0.1390	0.1427	0.1592
Blood	1.1171	1.0414	1.1538	1.4566	1.3843
W.A.T.	0.5319	1.4660	3.3439	1.7533	2.0514
Carcass	5.1328	4.9236	5.4938	5.0179	4.8861
Total body wt.	15.3784	15.1272	22.2710	17.0620	18.5982
Semilean body wt.	14.8465	13.6612	15.9271	15.3087	16.5468
Lean body wt.	14.4490	13.3141	14.6816	14.5875	15.7574

Table 7 (continued)

	Group C				
	31c	32c	33c	34c	35c
Skin	1.6777	1.7797	1.8983	1.4058	2.2336
Muscle ant. body	3.4457	3.3070	3.4197	2.9473	3.9883
Muscle post. body	1.2093	1.0039	1.1562	1.0284	1.3844
Total muscle	4.6550	4.3109	4.5759	3.9757	5.3727
Diaphragm	0.2233	0.0812	0.0769	0.0998	0.0943
Interscap. B.A.T.	0.2280	0.2427	0.1821	0.1622	0.1828
Other B.A.T.	0.4513	0.1841	0.2027	0.1432	0.1796
Total B.A.T.	0.6793	0.4268	0.3848	0.3054	0.3624
Liver	0.5610	0.4917	0.5504	0.4920	0.7066
Kidneys	0.1758	0.1521	0.1442	0.1645	0.1843
Stomach	0.1458	0.1080	0.1407	0.1029	0.1358
Intestine	0.6130	0.5457	0.5207	0.6217	0.8377
Myocardium	0.1282	0.1095	0.1337	0.1187	0.1176
Blood	1.0500	1.0701	1.1922	1.0350	1.3714
W.A.T.	0.4937	0.4697	1.3104	0.2036	1.9109
Carcass	4.6943	4.5837	4.7736	4.3653	5.2900
Total body wt.	15.0971	14.1291	15.7018	12.8904	18.6173
Semilean body wt.	14.6034	13.6594	14.3914	12.6868	16.7064
Lean body wt.	13.9241	13.2326	14.0066	12.3814	16.3440
	36c	37c	38c	39c	40c
Skin	1.6331	1.6614	1.8365	2.1712	1.8907
Muscle ant. body	2.9356	3.4995	4.3880	4.6297	3.5502
Muscle post. body	1.0823	1.2236	1.5715	1.5104	1.5187
Total muscle	4.0179	4.7231	5.9595	6.1401	5.0687
Diaphragm	0.0794	0.0810	0.1115	0.1145	0.0931
Interscap. B.A.T.	0.1530	0.2120	0.1764	0.2369	0.4785
Other B.A.T.	0.1260	0.1822	0.1862	0.1987	0.4677
Total B.A.T.	0.2790	0.3942	0.3626	0.4356	0.9462
Liver	0.5753	0.7520	0.6925	0.8040	0.8270
Kidneys	0.1483	0.1730	0.2047	0.1906	0.1502
Stomach	0.1172	0.0988	0.1881	0.1459	0.1264
Intestine	0.5240	0.5257	0.5082	0.5028	0.4827
Myocardium	0.1119	0.1174	0.1505	0.1502	0.1435
Blood	1.0411	1.0210	1.3250	1.5668	1.2351
W.A.T.	0.2417	3.1709	2.1399	2.8406	1.1227
Carcass	4.7785	4.6415	5.6972	5.9534	5.2262
Total body wt.	13.5474	17.3600	19.1762	21.0157	17.3127
Semilean body wt.	13.3057	14.1891	17.0363	18.1751	16.1900
Lean body wt.	13.0267	13.7949	16.6737	17.7395	15.2438

Table 7 (continued)

	Group C					
	41c	42c	43c	44c	45c	46c
Skin	1.4209	1.7870	1.9329	1.8273	2.2576	1.5728
Muscle ant. body	2.9275	4.6840	3.9736	3.9636	3.5659	3.0012
Muscle post. body	1.1285	1.4996	1.3331	1.4983	1.3723	1.1753
Total muscle	4.0560	6.1836	5.3067	5.4619	4.9382	4.1765
Diaphragm	0.0780	0.0951	0.0983	0.1029	0.0853	0.0825
Interscap. B.A.T.	0.1106	0.0851	0.2642	0.1407	0.2028	0.1059
Other B.A.T.	0.1425	0.0989	0.2440	0.1123	0.1997	0.0957
Total B.A.T.	0.2531	0.1840	0.5082	0.2530	0.4025	0.2016
Liver	0.6146	0.8138	0.5685	0.7490	0.6830	0.5318
Kidneys	0.1635	0.2250	0.1817	0.1958	0.1915	0.1698
Stomach	0.1131	0.1693	0.1616	0.1664	0.1617	0.1100
Intestine	0.5465	0.5218	0.3547	0.5110	0.8279	0.5605
Myocardium	0.1016	0.1391	0.1356	0.1321	0.1290	0.1078
Blood	1.0787	1.0814	1.1702	1.1500	1.1266	0.9080
W.A.T.	0.1996	0.1260	2.5242	0.1336	3.3226	0.0000
Carcass	4.4627	5.2504	5.0064	5.0970	5.3015	4.2572
Total body wt.	13.0883	16.5765	17.9490	15.7800	19.4274	12.6785
Semilean body wt.	12.8887	16.4505	15.4248	15.6464	16.1048	12.6785
Lean body wt.	12.6356	16.2665	14.9166	15.3934	15.7023	12.4769

	47c	48c	49c	Mean	s_d (±)
Skin	1.5822	1.7299	1.7237	1.7004	0.3092
Muscle ant. body	4.4324	4.0252	3.6437	3.6982	0.5168
Muscle post. body	1.3805	1.4612	1.2012	1.3145	0.1697
Total muscle	5.8129	5.4864	4.8449	5.0127	0.6638
Diaphragm	0.1096	0.1068	0.0989	0.0960	0.0223
Interscap. B.A.T.	0.1381	0.1879	0.2198	0.2279	0.1191
Other B.A.T.	0.1186	0.1567	0.1909	0.2263	0.1154
Total B.A.T.	0.2567	0.3446	0.4107	0.4542	0.2298
Liver	0.6371	0.7600	0.5327	0.6505	0.1028
Kidneys	0.2494	0.1888	0.1589	0.1804	0.0309
Stomach	0.1769	0.1295	0.1233	0.1411	0.0270
Intestine	0.4033	0.5898	0.4623	0.5432	0.1209
Myocardium	0.1317	0.1368	0.1319	0.1280	0.0149
Blood	1.4125	1.2325	1.3260	1.1570	0.1354
W.A.T.	0.3428	2.7604	1.6191	1.0621	0.9487
Carcass	4.9566	5.3213	4.5940	5.0145	0.4441
Total body wt.	16.0717	18.7868	16.0264	16.1401	1.9435
Semilean body wt.	15.7289	16.0264	14.4073	15.0780	1.4281
Lean body wt.	15.4722	15.6818	13.9966	14.6239	1.4135

Table 8. Organ and tissue weights (expressed as a percentage of semilean body weight) of *E. fuscus*, sacrificed at different heart rates during arousal from hibernation in the summer

	Group C				
	1c	2c	3c	4c	5c
Skin	9.94	11.71	10.38	14.20	11.55
Muscle ant. body	26.62	26.12	23.68	22.16	25.37
Muscle post. body	9.01	7.92	8.44	8.64	9.31
Total muscle	35.63	34.04	32.12	30.80	34.69
Diaphragm	0.69	0.66	0.65	0.53	0.67
Interscap. B.A.T.	1.45	1.51	1.82	1.38	1.58
Other B.A.T.	1.60	1.46	1.59	1.47	1.40
Total B.A.T.	3.04	2.97	3.41	2.85	2.98
Liver	4.41	4.68	4.95	4.13	4.34
Kidneys	1.21	1.53	1.59	1.14	1.06
Stomach	0.78	1.01	1.00	1.09	0.94
Intestine	3.83	3.88	4.45	5.34	2.68
Myocardium	0.76	0.63	0.74	0.80	0.92
Blood	7.59	7.09	7.81	6.76	7.32
Carcass	32.13	31.81	32.89	32.37	32.83
	6c	7c	8c	9c	10c
Skin	10.37	14.80	8.76	9.65	11.55
Muscle ant. body	24.79	24.15	26.58	23.89	24.18
Muscle post. body	9.39	8.12	8.14	8.62	9.11
Total muscle	34.18	32.27	34.71	32.51	33.30
Diaphragm	0.63	0.63	0.53	0.63	0.69
Interscap. B.A.T.	0.99	1.34	1.53	1.12	1.09
Other B.A.T.	0.94	1.17	1.56	1.04	1.06
Total B.A.T.	1.93	2.51	3.09	2.16	2.15
Liver	3.63	3.53	4.29	4.06	5.21
Kidneys	1.74	1.08	1.12	1.11	1.35
Stomach	0.97	0.87	1.01	0.75	1.10
Intestine	5.07	2.76	4.26	4.21	2.86
Myocardium	0.76	0.91	0.80	0.72	0.87
Blood	7.31	6.35	8.90	8.26	5.83
Carcass	33.40	34.29	32.54	35.95	35.10

Table 8 (continued)

	Group C				
	11c	12c	13c	14c	15c
Skin	10.12	9.45	9.93	10.43	12.52
Muscle ant. body	28.26	27.22	24.98	25.36	25.42
Muscle post. body	10.23	9.79	8.90	8.90	8.87
Total muscle	38.49	37.01	33.88	34.26	34.29
Diaphragm	0.70	0.62	0.55	0.59	0.53
Interscap. B.A.T.	0.63	0.98	1.12	1.36	1.25
Other B.A.T.	1.43	1.00	1.10	1.29	1.22
Total B.A.T.	2.06	1.98	2.22	2.65	2.47
Liver	3.56	3.63	3.61	4.76	4.21
Kidneys	1.16	1.36	1.34	1.13	1.14
Stomach	0.97	0.83	0.82	1.02	0.64
Intestine	2.79	2.67	3.43	2.82	3.35
Myocardium	0.76	0.90	0.81	0.88	0.82
Blood	6.85	7.62	8.71	7.47	6.72
Carcass	32.54	33.92	34.71	33.98	33.31
	16c	17c	18c	19c	20c
Skin	12.26	11.77	13.50	9.68	10.79
Muscle ant. body	22.51	24.09	23.11	25.78	23.73
Muscle post. body	8.59	8.60	8.69	9.08	8.81
Total muscle	31.10	32.69	31.79	34.86	32.54
Diaphragm	0.55	0.57	0.59	0.55	0.58
Interscap. B.A.T.	1.15	0.95	1.21	1.54	1.13
Other B.A.T.	1.34	0.98	1.15	1.56	1.24
Total B.A.T.	2.50	1.93	2.36	3.10	2.38
Liver	5.45	5.02	4.19	4.08	4.33
Kidneys	1.07	1.14	1.27	1.34	1.17
Stomach	0.78	0.90	0.72	0.82	0.77
Intestine	3.67	4.20	4.90	3.32	3.44
Myocardium	0.79	1.00	0.89	0.84	0.66
Blood	8.17	7.54	7.40	7.62	7.74
Carcass	33.67	33.24	32.38	33.79	35.60

Table 8 (continued)

	Group C				
	21c	22c	23c	24c	25c
Skin	11.07	12.61	8.30	8.99	8.27
Muscle ant. body	20.53	26.42	21.42	24.63	24.12
Muscle post. body	7.97	8.18	8.26	8.74	8.91
Total muscle	28.51	34.59	29.68	33.37	33.03
Diaphragm	0.67	0.65	0.64	0.76	0.71
Interscap. B.A.T.	4.95	2.55	1.47	2.14	2.23
Other B.A.T.	4.21	2.06	1.45	2.24	2.21
Total B.A.T.	9.16	4.61	2.92	4.38	4.44
Liver	4.94	3.56	6.09	3.75	3.72
Kidneys	1.28	0.91	1.44	1.08	1.01
Stomach	0.94	0.83	1.09	1.23	1.21
Intestine	4.26	2.97	4.58	3.29	3.18
Myocardium	0.91	0.86	0.95	1.01	1.00
Blood	7.35	6.86	8.69	7.64	8.48
Carcass	30.90	31.54	35.63	34.49	34.94
	26c	27c	28c	29c	30c
Skin	10.06	10.10	11.36	9.56	11.18
Muscle ant. body	26.48	23.20	19.53	23.79	25.95
Muscle post. body	8.64	8.48	8.55	8.16	9.52
Total muscle	35.11	31.68	28.07	31.96	35.47
Diaphragm	0.58	0.56	0.57	0.64	0.61
Interscap. B.A.T.	1.38	1.27	3.85	2.29	2.35
Other B.A.T.	1.30	1.27	3.97	2.42	2.42
Total B.A.T.	2.68	2.54	7.82	4.71	4.77
Liver	4.09	3.93	4.26	4.72	4.71
Kidneys	1.03	1.28	1.01	1.02	0.91
Stomach	1.06	0.92	1.35	1.01	1.04
Intestine	2.47	4.35	2.94	3.17	2.47
Myocardium	0.83	0.99	0.87	0.93	0.96
Blood	7.52	7.62	7.24	9.51	8.37
Carcass	34.57	36.04	34.49	32.78	29.53

Table 8 (continued)

	Group C				
	31c	32c	33c	34c	35c
Skin	11.49	13.03	13.19	11.08	13.37
Muscle ant. body	23.60	24.21	23.76	23.23	23.87
Muscle post. body	8.28	7.35	8.03	8.11	8.29
Total muscle	31.88	31.56	31.80	31.34	32.16
Diaphragm	1.53	0.59	0.53	0.79	0.56
Interscap. B.A.T.	1.56	1.78	1.27	1.28	1.09
Other B.A.T.	3.09	1.35	1.41	1.13	1.08
Total B.A.T.	4.65	3.12	2.67	2.41	2.17
Liver	3.84	3.60	3.82	3.88	4.23
Kidneys	1.20	1.11	1.00	1.30	1.10
Stomach	1.00	0.79	0.98	0.81	0.81
Intestine	4.20	4.00	3.62	4.90	5.01
Myocardium	0.88	0.80	0.93	0.94	0.70
Blood	7.19	7.83	8.28	8.16	8.21
Carcass	32.15	33.56	33.17	34.41	31.66
	36c	37c	38c	39c	40c
Skin	12.27	11.71	10.78	11.95	11.68
Muscle ant. body	22.06	24.66	25.76	25.47	21.93
Muscle post. body	8.13	8.62	9.22	8.31	9.38
Total muscle	30.20	33.29	34.98	33.78	31.31
Diaphragm	0.60	0.57	0.65	0.63	0.58
Interscap. B.A.T.	1.15	1.49	1.04	1.30	2.96
Other B.A.T.	0.95	1.28	1.09	1.09	2.89
Total B.A.T.	2.10	2.78	2.13	2.40	5.84
Liver	4.32	5.30	4.06	4.42	5.11
Kidneys	1.11	1.22	1.20	1.05	0.93
Stomach	0.88	0.70	1.10	0.80	0.78
Intestine	3.94	3.70	2.98	2.77	2.98
Myocardium	0.84	0.83	0.88	0.83	0.89
Blood	7.82	7.20	7.78	8.62	7.63
Carcass	35.91	32.71	33.44	32.76	32.28

Table 8 (continued)

	Group C					
	41c	42c	43c	44c	45c	46c
Skin	11.02	10.86	12.53	11.68	14.02	12.41
Muscle ant. body	22.71	28.47	25.76	25.33	22.14	23.67
Muscle post. body	8.76	9.12	8.64	9.58	8.52	9.27
Total muscle	31.47	37.59	34.40	34.91	30.66	32.94
Diaphragm	0.61	0.58	0.64	0.66	0.53	0.65
Interscap. B.A.T.	0.86	0.52	1.71	0.90	1.26	0.84
Other B.A.T.	1.11	0.60	1.58	0.72	1.24	0.75
Total B.A.T.	1.96	1.12	3.29	1.62	2.50	1.59
Liver	4.77	4.95	3.69	4.79	4.24	4.19
Kidneys	1.27	1.37	1.18	1.25	1.19	1.34
Stomach	0.88	1.03	1.05	1.06	1.00	0.87
Intestine	4.24	3.17	2.30	3.27	5.14	4.42
Myocardium	0.79	0.85	0.88	0.84	0.80	0.85
Blood	8.37	6.57	7.59	7.35	7.00	7.16
Carcass	34.62	31.92	32.46	32.58	32.92	33.58

	47c	48c	49c	Mean	s_d (±)
Skin	10.06	10.79	11.96	11.24	1.50
Muscle ant. body	28.18	25.12	25.29	24.48	1.90
Muscle post. body	8.78	9.12	8.34	8.70	0.54
Total muscle	36.96	34.23	33.63	33.18	2.17
Diaphragm	0.70	0.67	0.69	0.64	0.14
Interscap. B.A.T.	0.88	1.17	1.53	1.51	0.77
Other B.A.T.	0.75	0.98	1.33	1.50	0.75
Total B.A.T.	1.63	2.15	2.85	3.01	1.50
Liver	4.05	4.74	3.70	4.32	0.58
Kidneys	1.59	1.18	1.10	1.20	0.17
Stomach	1.12	0.81	0.86	0.93	0.14
Intestine	2.56	3.68	3.21	3.63	0.81
Myocardium	0.84	0.85	0.92	0.85	0.08
Blood	8.98	7.69	9.20	7.69	0.74
Carcass	31.51	33.20	31.89	33.31	1.40

Table 9. Organ and tissue weights (expressed as a percentage of lean body weight) of *E. fuscus*, sacrificed at different heart rates during arousal from hibernation in the summer

	Group C				
	1c	2c	3c	4c	5c
Skin	10.25	12.07	10.75	14.61	11.91
Muscle ant. body	27.46	26.92	24.51	22.81	26.15
Muscle post. body	9.30	8.16	8.74	8.90	9.60
Total muscle	36.75	35.08	33.25	31.70	35.75
Diaphragm	0.71	0.68	0.68	0.54	0.69
Liver	4.55	4.83	5.12	4.25	4.47
Kidneys	1.25	1.58	1.65	1.17	1.09
Stomach	0.80	1.04	1.04	1.13	0.97
Intestine	3.95	3.99	4.60	5.49	2.77
Myocardium	0.78	0.65	0.77	0.82	0.95
Blood	7.83	7.31	8.09	6.96	7.55
Carcass	33.13	32.78	34.05	33.32	33.84
	6c	7c	8c	9c	10c
Skin	10.58	15.18	9.04	9.86	11.80
Muscle ant. body	25.28	24.77	27.42	24.42	24.71
Muscle post. body	9.58	8.33	8.40	8.81	9.31
Total muscle	34.85	33.10	35.82	33.23	34.03
Diaphragm	0.64	0.64	0.54	0.65	0.71
Liver	3.70	3.62	4.43	4.15	5.33
Kidneys	1.78	1.11	1.15	1.13	1.38
Stomach	0.99	0.89	1.04	0.76	1.12
Intestine	5.17	2.83	4.39	4.31	2.92
Myocardium	0.78	0.94	0.82	0.74	0.89
Blood	7.46	6.52	9.18	8.44	5.95
Carcass	34.06	35.17	33.58	36.74	35.87

Table 9 (continued)

	Group C				
	11c	12c	13c	14c	15c
Skin	10.33	9.64	10.15	10.71	12.83
Muscle ant. body	28.86	27.77	25.54	26.05	26.06
Muscle post. body	10.45	9.99	9.10	9.14	9.10
Total muscle	39.30	37.76	34.65	35.20	35.16
Diaphragm	0.72	0.64	0.56	0.61	0.54
Liver	3.63	3.70	3.70	4.89	4.32
Kidneys	1.19	1.39	1.37	1.16	1.17
Stomach	0.99	0.85	0.84	1.05	0.66
Intestine	2.85	2.73	3.50	2.90	3.44
Myocardium	0.77	0.92	0.83	0.90	0.84
Blood	6.99	7.77	8.91	7.68	6.89
Carcass	33.23	34.61	35.50	34.91	34.16
	16c	17c	18c	19c	20c
Skin	12.58	12.00	13.83	9.99	11.05
Muscle ant. body	23.08	24.56	23.67	26.60	24.30
Muscle post. body	8.81	8.77	8.90	9.37	9.02
Total muscle	31.89	33.33	32.56	35.97	33.33
Diaphragm	0.56	0.59	0.60	0.56	0.59
Liver	5.59	5.12	4.29	4.22	4.44
Kidneys	1.10	1.16	1.30	1.38	1.20
Stomach	0.80	0.92	0.74	0.85	0.79
Intestine	3.77	4.28	5.02	3.43	3.53
Myocardium	0.81	1.02	0.92	0.87	0.68
Blood	8.38	7.68	7.58	7.86	7.93
Carcass	34.53	33.90	33.16	34.87	36.46

Table 9 (continued)

	Group C				
	21c	22c	23c	24c	25c
Skin	12.19	13.22	8.55	9.40	8.66
Muscle ant. body	22.61	27.69	22.06	25.75	25.24
Muscle post. body	8.78	8.57	8.51	9.14	9.33
Total muscle	31.38	36.27	30.57	34.90	34.57
Diaphragm	0.74	0.69	0.66	0.80	0.74
Liver	5.44	3.73	6.27	3.93	3.89
Kidneys	1.41	0.96	1.48	1.13	1.06
Stomach	1.03	0.87	1.12	1.29	1.27
Intestine	4.69	3.12	4.72	3.44	3.33
Myocardium	1.00	0.91	0.98	1.06	1.05
Blood	8.10	7.19	8.95	7.99	8.88
Carcass	34.02	33.06	36.70	36.07	36.57
	26c	27c	28c	29c	30c
Skin	10.33	10.36	12.32	10.03	11.74
Muscle ant. body	27.20	23.80	21.18	24.97	27.25
Muscle post. body	8.87	8.70	9.27	8.57	10.00
Total muscle	36.08	32.50	30.45	33.54	37.25
Diaphragm	0.59	0.57	0.62	0.67	0.64
Liver	4.20	4.04	4.62	4.95	4.94
Kidneys	1.06	1.31	1.10	1.07	0.95
Stomach	1.09	0.94	1.47	1.06	1.09
Intestine	2.54	4.46	3.19	3.32	2.59
Myocardium	0.86	1.02	0.95	0.98	1.01
Blood	7.73	7.82	7.86	9.99	8.79
Carcass	35.52	36.98	37.42	34.40	31.01

Table 9 (continued)

	Group C				
	31c	32c	33c	34c	35c
Skin	12.05	13.45	13.55	11.35	13.67
Muscle ant. body	24.75	24.99	24.41	23.80	24.40
Muscle post. body	8.68	7.59	8.25	8.31	8.47
Total muscle	33.43	32.58	32.67	32.11	32.87
Diaphragm	1.60	0.61	0.55	0.81	0.58
Liver	4.03	3.72	3.93	3.97	4.32
Kidneys	1.26	1.15	1.03	1.33	1.13
Stomach	1.05	0.82	1.00	0.83	0.83
Intestine	4.40	4.12	3.72	5.02	5.13
Myocardium	0.92	0.83	0.95	0.96	0.72
Blood	7.54	8.09	8.51	8.36	8.39
Carcass	33.71	34.64	34.08	35.26	32.37
	36c	37c	38c	39c	40c
Skin	12.54	12.04	11.01	12.24	12.40
Muscle ant. body	22.54	25.37	26.32	26.10	23.29
Muscle post. body	8.31	8.87	9.43	8.51	9.96
Total muscle	30.84	34.24	35.74	34.61	33.25
Diaphragm	0.61	0.59	0.67	0.65	0.61
Liver	4.42	5.45	4.15	4.53	5.43
Kidneys	1.14	1.25	1.23	1.07	0.99
Stomach	0.90	0.72	1.13	0.82	0.83
Intestine	4.02	3.81	3.05	2.83	3.17
Myocardium	0.86	0.85	0.90	0.85	0.94
Blood	7.99	7.40	7.95	8.83	8.10
Carcass	36.68	33.65	34.17	33.56	34.28

Table 9 (continued)

	Group C					
	41c	42c	43c	44c	45c	46c
Skin	11.25	10.99	12.96	11.87	14.38	12.61
Muscle ant. body	23.17	28.80	26.64	25.75	22.71	24.05
Muscle post. body	8.93	9.22	8.94	9.73	8.74	9.42
Total muscle	32.10	38.01	35.58	35.48	31.45	33.47
Diaphragm	0.62	0.58	0.66	0.67	0.54	0.66
Liver	4.86	5.00	3.81	4.87	4.35	4.26
Kidneys	1.29	1.38	1.22	1.27	1.22	1.36
Stomach	0.90	1.04	1.08	1.08	1.03	0.88
Intestine	4.33	3.21	2.38	3.32	5.27	4.49
Myocardium	0.80	0.86	0.91	0.86	0.82	0.86
Blood	8.54	6.65	7.84	7.47	7.17	7.28
Carcass	35.32	32.28	33.56	33.11	33.76	34.12

	47c	48c	49c	Mean	s_d (±)
Skin	10.23	11.03	12.32	11.59	1.54
Muscle ant. body	28.65	25.67	26.03	25.23	1.81
Muscle post. body	8.92	9.32	8.58	8.97	0.54
Total muscle	37.57	34.99	34.61	34.20	2.04
Diaphragm	0.71	0.68	0.71	0.66	0.15
Liver	4.12	4.85	3.81	4.45	0.60
Kidneys	1.61	1.20	1.14	1.24	0.17
Stomach	1.14	0.83	0.88	0.96	0.16
Intestine	2.61	3.76	3.30	3.74	0.83
Myocardium	0.85	0.87	0.94	0.88	0.09
Blood	9.13	7.86	9.47	7.93	0.78
Carcass	32.04	33.93	32.82	34.34	1.41

APPENDIX 3

PERCENTAGES (%) OF INJECTED 86-Rb (RUBIDIUM) REMAINING PER 1 ML OF BLOOD OF *E. FUSCUS*, SACRIFICED DURING DIFFERENT PHYSIOLOGICAL STATES

Table 1. Percentages of injected 86-Rb remaining per 1 ml of blood of *E. fuscus*, sacrificed at heart rates 40 beats per minute (Graph A; Fig. 19). Sixty, 120, 240, and 480 heart beats passed between 86-Rb and KCl injections.

ANIMAL NUMBER	PERCENTAGE OF 86-Rb REMAINING PER 1 ML OF BLOOD			
	Number of heart beats passed between 86-Rb and KCl injections			
	60	120	240	480
1	13.50	10.03	7.70	4.50
2	13.31	9.69	7.57	
3	18.29	9.34	8.44	
4	17.01	10.79	7.94	
5		9.72	6.80	
6		11.97	9.90	
7		10.45		
8		10.93		
Mean	15.53	10.37	8.05	
s_d (±)	2.51	0.86	1.04	

Table 2. Percentages of injected 86-Rb remaining per 1 ml of blood of *E. fuscus*, sacrificed at heart rates 480 beats per minute (Graph B; Fig. 19). Sixty, 120, 240, and 480 heart beats passed between 86-Rb and KCl injections.

ANIMAL NUMBER	PERCENTAGE OF 86-Rb REMAINING PER 1 ML OF BLOOD			
	Number of heart beats passed between 86-Rb and KCl injections			
	60	120	240	480
1	13.85	9.73	6.95	4.43
2	15.06	10.27	7.04	
3	18.02	10.73	7.89	
4	11.47	6.97	7.82	
5		9.09	8.05	
6		9.65	7.98	
7		9.67		
8		8.72		
Mean	14.60	9.35	7.62	
sd (±)	2.72	1.15	0.49	

Table 3. Percentages of injected 86-Rb remaining per 1 ml of blood of *E.* during arousal from hibernation, and during post-arousal (rest- and twenty heart beats passed between 86-Rb and KCl injections.

	PERCENTAGE OF 86-Rb				
Animal no.	Deep hibernation (T_a = 5 C)	Arousal from hibernation			
					HEART
	12	40	80	120	180
1	12.80	10.03	9.51	9.24	10.80
2	11.24	9.69	9.83	11.60	9.09
3	10.16	9.34	12.60	12.96	11.30
4	11.12	10.79	12.73	8.44	7.71
5	9.80	9.72	10.62	7.20	8.32
6	9.28	11.98	7.99	11.04	9.38
7		10.45	9.24	11.14	11.20
8		10.93	10.94	9.49	11.00
Mean	10.74	10.37	10.43	10.14	9.85
s_d (±)	1.26	0.86	1.64	1.88	1.41
		Arousal from hibernation			
1	9.71	12.91	10.17	13.74	7.56
2	8.76	13.86	9.76	15.51	8.51
3	12.90	9.76	8.10	13.72	10.07
4	9.52	10.85	12.86	12.65	9.40
5	9.57			12.93	
Mean	10.09	11.88	10.22	13.71	8.88
s_d (±)	1.61	1.83	1.97	1.11	1.09

fuscus, sacrificed during deep hibernation, at different heart rates ing) in the winter (Graph C; Fig. 20) and in the summer. One hundred

PER 1 ML OF BLOOD						
(T_a = 5 C) in the winter						Post-arousal (T_a = 22 C)
RATES						
240	300	360	480	600	800	480
5.68	8.50	8.95	9.73	9.05	10.36	8.14
11.41	8.26	9.14	10.27	6.75	8.27	12.09
9.26	9.51	7.20	10.73	9.20	7.04	9.05
5.04	7.56	10.03	6.98	10.50	6.96	9.42
11.35	8.81	9.00	9.09	9.96	6.44	7.93
9.80	12.45	7.76	9.65	10.36	6.82	10.18
9.60	10.73	10.44	9.67	9.86	10.23	9.37
8.53	9.44	9.68	8.73	10.38	8.78	9.44
8.84	9.41	9.03	9.36	9.51	8.11	9.46
2.36	1.56	1.10	1.14	1.24	1.55	1.40
(T_a = 5 C) in the summer						
					HR = 740	
11.59		7.93	10.16	11.27	10.90	10.56
14.16		8.54	7.46	7.32	7.90	6.08
11.96		8.92	8.76	6.22	9.08	10.04
9.84		11.91	9.86	9.06	9.30	7.49
10.27			11.49		8.10	
11.56		9.33	9.55	8.47	9.06	8.54
1.70		1.77	1.52	2.20	1.20	2.12

Table 4. Percentages of injected 86-Rb remaining per 1 ml of blood of single individuals (*E. fuscus*), sacrificed at different heart rates (Graph D; Fig. 20) during the arousal from hibernation (T_a = 5 C). Sixty seconds passed between 86-Rb and KCl injections.

Animal number	*E. fuscus* sacrificed at heart rates (beats/min)	Percentage 86-Rb per 1 ml blood
1	20	21.05
2	60	15.57
3	120	10.45
4	240	8.47
5	360	5.69
6	480	4.38
7	600	4.42
8	800	3.63

Table 5. Percentages of injected 86-Rb remaining per 1 ml of blood of non-hibernating, lightly anaesthetized *E. fuscus*, sacrificed at heart rates 304 to 366 beats per minute in the warm (T_a = 22 C). One hundred and twenty heart beats passed between 86-Rb and KCl injections.

Animal number	*E. fuscus* sacrificed at heart rates (beats/min)	Percentage 86-Rb per 1 ml blood
1	320	11.69
2	304	10.20
3	366	12.84
4	364	7.70
5	340	9.72
6	320	11.55
7	344	8.59
8	320	9.73
9	320	9.35
10	350	6.73
Mean	335	9.81
s_d (±)	21	1.88

APPENDIX 4

PERCENTAGE OF INJECTED 86-Rb (RUBIDIUM) PER ORGAN OR TISSUE OF *E. FUSCUS*, SACRIFICED DURING DIFFERENT PHYSIOLOGICAL STATES, AND DIFFERENT SEASONS OF THE YEAR

Table 1. Percentage of injected 86-Rb per organ or tissue of non-hibernating, lightly anaesthetized *E. fuscus*, sacrificed in the summer

	Group A					
	1a	2a	3a	4a	5a	6a
Skin	8.30	10.32	14.60	14.72	13.30	8.29
Muscle ant. body	14.29	19.97	11.71	13.26	11.97	11.91
Muscle post. body	13.35	9.84	8.42	7.58	9.41	9.06
Total muscle	27.64	29.81	20.13	20.84	21.38	20.97
Diaphragm	1.25	1.05	0.77	0.81	1.10	1.23
Interscap. B.A.T.	2.16	1.98	1.07	0.36	2.31	0.23
Other B.A.T.	1.88	1.39	0.94	0.69	1.76	0.52
Total B.A.T.	4.04	3.37	2.01	1.05	4.07	0.75
Liver	3.84	5.32	6.29	6.01	7.20	6.84
Kidneys	2.78	2.29	2.18	4.58	2.46	4.69
Stomach	3.24	2.89	3.30	3.09	2.54	2.83
Intestine	5.46	4.00	5.28	7.73	5.65	6.05
Myocardium	4.98	3.80	3.38	4.97	4.11	7.66
Blood	12.54	10.42	12.24	8.75	11.33	12.12
W.A.T.	1.92	2.96	1.88	1.28	1.32	1.00
Carcass	24.01	23.77	27.93	26.16	25.54	27.58
	7a	8a	9a	10a	Mean	s_d (±)
Skin	12.42	11.87	12.65	10.36	11.68	2.32
Muscle ant. body	12.82	9.95	10.97	16.82	13.37	3.00
Muscle post. body	9.18	8.82	10.40	8.60	9.47	1.57
Total muscle	22.00	18.77	21.37	25.42	22.83	3.57
Diaphragm	0.94	1.10	1.36	1.30	1.09	0.20
Interscap. B.A.T.	0.46	0.39	0.40	0.71	1.00	0.82
Other B.A.T.	0.73	0.55	0.53	0.88	0.99	0.51
Total B.A.T.	1.19	0.94	0.93	1.59	1.99	1.33
Liver	6.72	6.20	7.97	5.68	6.21	1.13
Kidneys	2.43	1.22	3.13	4.28	3.00	1.16
Stomach	3.06	2.26	3.39	2.52	2.91	0.37
Intestine	6.03	7.15	8.26	5.06	6.07	1.30
Myocardium	4.03	4.78	3.12	6.29	4.71	1.39
Blood	9.82	10.83	9.93	7.79	10.58	1.55
W.A.T.	0.20	1.92	1.44	1.64	1.56	0.72
Carcass	31.15	32.96	27.45	28.05	27.46	2.90

Table 2. Percentage of injected 86-Rb per organ or tissue of *E. fuscus*, sacrificed at different heart rates during arousal from hibernation in the winter

	Group B			
	Subgroup 1: sacrificed at HR = 12 beats/min (deep hibernation)			
	1b	2b	3b	4b
Skin	6.00	5.42	6.40	5.35
Muscle ant. body	23.29	22.47	24.02	23.40
Muscle post. body	9.83	9.99	9.80	10.53
Total muscle	33.12	32.46	33.82	33.93
Diaphragm	0.70	0.68	0.58	0.81
Interscap. B.A.T.	2.46	3.18	2.46	2.36
Other B.A.T.	2.19	3.08	2.87	2.32
Total B.A.T.	4.65	6.26	5.33	4.68
Liver	5.97	5.67	4.81	4.59
Kidneys	1.56	1.43	0.90	0.92
Stomach	1.04	1.04	0.80	1.15
Intestine	4.74	6.22	4.60	5.69
Myocardium	2.41	2.80	2.40	2.71
Blood	18.16	16.37	14.50	14.87
W.A.T.	0.91	2.78	6.03	4.11
Carcass	20.74	18.87	19.82	21.20
	5b	6b	Mean	s_d (±)
Skin	4.94	6.10	5.70	0.55
Muscle ant. body	23.40	20.96	22.92	1.08
Muscle post. body	9.20	10.54	9.98	0.51
Total muscle	32.60	31.50	32.91	0.92
Diaphragm	0.78	0.77	0.72	0.08
Interscap. B.A.T.	3.06	2.28	2.63	0.38
Other B.A.T.	3.15	1.97	2.60	0.50
Total B.A.T.	6.21	4.25	5.23	0.85
Liver	5.08	4.68	5.13	0.56
Kidneys	1.15	1.38	1.22	0.28
Stomach	1.27	1.57	1.14	0.30
Intestine	5.55	4.12	5.15	0.79
Myocardium	3.58	2.60	2.75	0.44
Blood	13.47	14.09	15.24	1.73
W.A.T.	5.06	6.60	4.25	2.13
Carcass	20.30	22.33	20.54	1.19

Table 2 (continued)

	Group B Subgroup 2: sacrificed at HR = 40 beats/min (arousal)				
	7b	8b	9b	10b	11b
Skin	3.35	2.99	3.65	3.44	3.13
Muscle ant. body	34.70	35.42	38.45	32.13	32.15
Muscle post. body	10.25	8.60	9.68	9.38	9.26
Total muscle	44.95	44.02	48.13	41.51	41.41
Diaphragm	0.59	0.69	0.79	0.79	0.69
Interscap. B.A.T.	5.85	4.39	3.14	3.34	8.84
Other B.A.T.	6.07	3.50	2.83	3.16	5.99
Total B.A.T.	11.92	7.89	5.97	6.50	14.83
Liver	2.13	3.06	1.65	2.49	2.34
Kidneys	0.45	0.56	0.52	0.61	0.61
Stomach	0.24	0.30	0.31	0.53	0.76
Intestine	1.16	0.73	0.86	1.36	1.53
Myocardium	2.30	2.82	2.39	2.14	3.38
Blood	16.31	18.36	15.19	18.69	14.10
W.A.T.	1.59	1.69	2.49	1.90	1.50
Carcass	15.01	16.88	18.06	20.04	15.73
	12b	13b	14b	Mean	s_d (±)
Skin	2.61	2.56	4.22	3.24	0.55
Muscle ant. body	32.63	35.34	33.44	34.28	2.16
Muscle post. body	9.74	9.76	9.58	9.53	0.48
Total muscle	42.37	45.10	43.02	43.81	2.25
Diaphragm	0.73	0.84	0.88	0.75	0.09
Interscap. B.A.T.	5.95	6.13	5.66	5.41	1.82
Other B.A.T.	5.95	5.99	5.52	4.88	1.44
Total B.A.T.	11.90	12.12	11.18	10.29	3.13
Liver	3.12	1.53	2.64	2.37	0.59
Kidneys	0.47	0.51	0.43	0.52	0.07
Stomach	0.28	0.31	0.31	0.38	0.18
Intestine	0.91	0.49	0.77	0.98	0.35
Myocardium	1.91	2.20	1.81	2.37	0.51
Blood	16.25	16.48	15.64	16.38	1.53
W.A.T.	2.15	1.64	2.72	1.96	0.45
Carcass	17.31	16.19	17.37	17.07	1.55

Table 2 (continued)

	Group B				
	Subgroup 3: sacrificed at HR = 80 beats/min (arousal)				
	15b	16b	17b	18b	19b
Skin	2.67	2.87	2.98	2.99	2.30
Muscle ant. body	29.73	27.97	27.46	27.80	30.13
Muscle post. body	7.26	6.93	5.14	5.17	7.02
Total muscle	36.99	34.90	32.60	32.97	37.15
Diaphragm	0.68	0.61	0.71	0.70	0.62
Interscap. B.A.T.	11.78	14.95	13.06	13.10	14.15
Other B.A.T.	8.37	11.11	8.84	8.82	11.06
Total B.A.T.	20.15	26.06	21.90	21.92	25.21
Liver	2.53	2.01	2.21	2.20	1.65
Kidneys	0.59	0.67	0.53	0.56	0.61
Stomach	0.31	0.29	0.27	0.29	0.45
Intestine	0.71	1.15	0.38	0.38	0.82
Myocardium	2.38	3.09	2.91	2.86	3.01
Blood	15.25	11.90	20.16	20.04	11.84
W.A.T.	2.42	1.87	1.42	1.40	1.58
Carcass	15.32	14.57	13.92	13.69	14.76
	20b	21b	22b	Mean	s_d (±)
Skin	2.66	2.66	2.83	2.74	0.22
Muscle ant. body	30.33	31.07	30.28	29.35	1.38
Muscle post. body	9.25	8.26	8.16	7.15	1.45
Total muscle	39.58	39.33	38.44	36.50	2.73
Diaphragm	0.86	0.77	0.80	0.72	0.09
Interscap. B.A.T.	10.97	10.80	10.08	12.36	1.72
Other B.A.T.	7.76	6.89	6.99	8.73	1.63
Total B.A.T.	18.73	17.69	17.07	21.09	3.32
Liver	1.88	2.50	1.92	2.12	0.29
Kidneys	0.48	0.86	0.64	0.62	0.12
Stomach	0.33	0.35	0.25	0.32	0.06
Intestine	1.56	1.04	1.08	0.89	0.40
Myocardium	2.43	3.63	2.35	2.83	0.44
Blood	12.60	16.21	17.51	15.69	3.41
W.A.T.	1.69	2.06	2.12	1.82	0.36
Carcass	17.23	12.90	14.99	14.67	1.30

Table 2 (continued)

	Group B				
	Subgroup 4: sacrificed at HR = 120 beats/min (arousal)				
	23b	24b	25b	26b	27b
Skin	2.78	2.17	1.94	2.63	2.06
Muscle ant. body	33.76	34.92	37.71	32.41	35.78
Muscle post. body	6.62	7.19	5.21	6.47	6.55
Total muscle	40.38	42.11	42.92	38.88	42.33
Diaphragm	0.57	0.90	0.97	0.65	0.50
Interscap. B.A.T.	6.57	9.69	11.53	11.72	13.33
Other B.A.T.	7.72	7.59	7.62	11.02	10.98
Total B.A.T.	14.29	17.28	19.15	22.74	24.31
Liver	2.66	1.29	2.75	3.05	1.18
Kidneys	0.55	0.49	0.37	0.44	0.30
Stomach	0.32	0.29	0.25	0.29	0.26
Intestine	0.67	0.45	0.45	0.50	0.45
Myocardium	3.80	2.78	3.24	3.83	2.67
Blood	14.40	16.01	14.94	11.96	10.16
W.A.T.	1.58	1.45	0.83	1.85	1.71
Carcass	18.00	14.78	12.19	13.19	14.06
	28b	29b	30b	Mean	s_d (±)
Skin	2.03	2.71	2.77	2.39	0.37
Muscle ant. body	35.20	31.86	36.13	34.72	1.96
Muscle post. body	7.16	6.35	7.48	6.63	0.70
Total muscle	42.36	38.21	43.61	41.34	1.98
Diaphragm	0.83	0.63	0.73	0.72	0.16
Interscap. B.A.T.	9.36	11.51	7.45	10.14	2.31
Other B.A.T.	8.87	10.80	8.01	9.08	1.59
Total B.A.T.	18.23	22.31	15.46	19.22	3.61
Liver	1.94	1.81	1.83	2.06	0.69
Kidneys	0.32	0.43	0.59	0.44	0.10
Stomach	0.21	0.30	0.28	0.28	0.03
Intestine	0.42	0.50	0.58	0.50	0.08
Myocardium	3.26	3.79	3.26	3.33	0.45
Blood	14.07	15.02	14.56	13.89	1.90
W.A.T.	1.97	1.54	2.04	1.62	0.38
Carcass	14.35	12.89	14.28	14.22	1.76

Table 2 (continued)

	Group B Subgroup 5: sacrificed at HR = 180 beats/min (arousal)				
	31b	32b	33b	34b	35b
Skin	2.83	2.77	2.57	4.40	3.70
Muscle ant. body	32.59	30.12	31.32	32.61	34.84
Muscle post. body	3.59	5.53	4.57	5.82	3.25
Total muscle	36.18	35.65	35.89	38.43	38.09
Diaphragm	0.61	0.94	0.87	0.92	0.83
Interscap. B.A.T.	11.90	12.50	10.25	10.13	11.27
Other B.A.T.	9.39	11.42	10.50	8.15	9.64
Total B.A.T.	21.29	23.92	20.75	18.28	20.91
Liver	1.62	1.32	1.30	1.02	0.99
Kidneys	0.37	0.47	0.42	0.37	0.33
Stomach	0.30	0.41	0.30	0.26	0.29
Intestine	0.54	0.50	0.53	0.61	0.49
Myocardium	4.26	5.34	4.82	3.64	4.17
Blood	15.02	13.65	11.88	12.76	12.00
W.A.T.	1.62	1.29	2.24	1.88	2.61
Carcass	15.36	13.72	18.43	17.44	15.59
	36b	37b	38b	Mean	s_d (±)
Skin	2.81	2.83	2.54	3.06	0.65
Muscle ant. body	36.95	33.73	30.87	32.88	2.25
Muscle post. body	4.50	4.48	5.14	4.61	0.89
Total muscle	41.45	38.21	36.01	37.49	1.97
Diaphragm	0.59	0.57	0.75	0.76	0.15
Interscap. B.A.T.	11.39	14.09	11.86	11.67	1.27
Other B.A.T.	7.70	7.13	9.20	9.14	1.44
Total B.A.T.	19.09	21.22	21.06	20.81	1.67
Liver	1.38	1.41	1.70	1.34	0.25
Kidneys	0.39	0.39	0.55	0.41	0.07
Stomach	0.27	0.27	0.39	0.31	0.06
Intestine	0.51	0.51	0.57	0.53	0.04
Myocardium	4.69	4.66	4.52	4.51	0.50
Blood	11.37	13.49	13.77	12.99	1.21
W.A.T.	1.54	0.30	0.96	1.55	0.73
Carcass	15.92	16.13	17.20	16.22	1.45

Table 2 (continued)

	Group B				
	Subgroup 6: sacrificed at HR = 240 beats/min (arousal)				
	39b	40b	41b	42b	43b
Skin	2.74	2.11	2.60	2.75	2.96
Muscle ant. body	33.86	33.77	35.74	30.05	35.84
Muscle post. body	3.17	4.20	3.64	4.32	4.35
Total muscle	37.03	37.97	39.38	34.37	40.19
Diaphragm	0.89	1.00	0.75	0.50	0.92
Interscap. B.A.T.	17.56	13.41	13.32	16.75	9.79
Other B.A.T.	13.84	11.12	9.60	13.87	9.61
Total B.A.T.	31.40	24.53	22.92	30.62	19.40
Liver	0.88	1.92	0.97	1.70	1.41
Kidneys	1.01	0.45	0.32	0.47	0.44
Stomach	0.29	0.34	0.27	0.22	0.31
Intestine	0.67	0.51	0.56	0.47	0.53
Myocardium	4.65	4.27	4.04	3.66	4.05
Blood	8.49	14.23	14.07	7.76	14.79
W.A.T.	1.32	0.95	1.35	2.64	1.69
Carcass	10.61	11.72	12.75	14.84	13.32
	44b	45b	46b	Mean	s_d (±)
Skin	2.19	2.20	2.64	2.52	0.32
Muscle ant. body	35.41	37.47	36.07	34.78	2.25
Muscle post. body	4.46	4.38	3.77	4.04	0.46
Total muscle	39.87	41.85	39.84	38.81	2.31
Diaphragm	0.91	0.85	0.77	0.82	0.15
Interscap. B.A.T.	11.44	14.24	13.40	13.74	2.54
Other B.A.T.	9.05	6.46	9.63	10.40	2.50
Total B.A.T.	20.49	20.70	23.03	24.13	4.55
Liver	1.24	1.02	0.99	1.27	0.40
Kidneys	0.50	0.30	0.33	0.48	0.23
Stomach	0.24	0.25	0.29	0.28	0.04
Intestine	0.40	0.35	0.56	0.51	0.10
Myocardium	3.65	4.63	4.09	4.13	0.40
Blood	14.37	12.23	13.26	12.40	2.80
W.A.T.	1.40	1.11	1.50	1.50	0.51
Carcass	14.74	14.50	12.69	13.14	1.52

Table 2 (continued)

	Group B				
	Subgroup 8: sacrificed at HR = 360 beats/min (arousal)				
	55b	56b	57b	58b	59b
Skin	2.50	2.65	2.09	2.26	3.76
Muscle ant. body	33.98	36.85	38.65	35.91	40.68
Muscle post. body	2.89	4.30	3.55	5.45	4.17
Total muscle	36.87	41.15	42.20	41.36	44.85
Diaphragm	0.70	0.79	1.35	1.04	0.93
Interscap. B.A.T.	11.01	8.62	12.60	8.64	6.74
Other B.A.T.	8.40	7.17	9.61	9.53	6.23
Total B.A.T.	19.41	15.79	22.21	18.17	12.97
Liver	1.57	1.71	1.01	1.73	1.36
Kidneys	0.42	0.41	0.17	0.45	0.42
Stomach	0.26	0.30	0.33	0.24	0.51
Intestine	0.40	0.45	0.67	0.45	0.91
Myocardium	4.86	5.51	6.24	4.20	4.76
Blood	15.61	12.42	9.69	12.96	12.12
W.A.T.	1.48	1.12	1.06	0.71	0.83
Carcass	15.92	17.69	13.09	16.44	16.59
	60b	61b	62b	Mean	s_d (±)
Skin	2.87	2.60	3.65	2.80	0.61
Muscle ant. body	31.07	34.92	39.58	36.48	3.20
Muscle post. body	6.27	3.42	4.04	4.26	1.11
Total muscle	37.34	38.34	43.62	40.72	2.93
Diaphragm	0.74	0.86	1.19	0.95	0.23
Interscap. B.A.T.	10.86	10.31	6.36	9.39	2.18
Other B.A.T.	8.36	6.13	5.96	7.67	1.50
Total B.A.T.	19.22	16.44	12.32	17.07	3.36
Liver	1.78	2.33	1.29	1.60	0.40
Kidneys	0.40	0.71	0.41	0.42	0.14
Stomach	0.21	0.42	0.48	0.34	0.11
Intestine	0.47	0.76	0.85	0.62	0.20
Myocardium	3.73	5.24	4.27	4.85	0.81
Blood	13.45	15.12	15.14	13.31	1.98
W.A.T.	2.96	1.75	0.80	1.34	0.74
Carcass	16.83	15.44	15.99	15.97	1.35

Table 2 (continued)

	Group B				
	Subgroup 9: sacrificed at HR = 480 beats/min (arousal)				
	63b	64b	65b	66b	67b
Skin	1.87	2.53	2.22	2.70	3.18
Muscle ant. body	35.10	35.52	34.38	41.38	33.92
Muscle post. body	3.11	2.53	2.47	2.20	2.60
Total muscle	38.21	38.05	36.85	43.58	36.52
Diaphragm	0.94	0.65	0.78	1.42	0.89
Interscap. B.A.T.	10.97	9.22	12.98	10.72	9.99
Other B.A.T.	10.82	6.97	9.19	8.91	8.89
Total B.A.T.	21.79	16.19	22.17	19.63	18.88
Liver	3.15	1.97	1.85	1.14	1.51
Kidneys	0.71	0.56	0.78	0.77	0.63
Stomach	0.32	0.37	0.27	0.62	0.46
Intestine	0.77	1.18	0.79	1.15	0.63
Myocardium	6.24	6.88	5.85	6.34	4.88
Blood	14.21	14.81	15.03	9.43	13.10
W.A.T.	1.14	1.12	0.75	0.50	1.30
Carcass	10.67	15.68	12.66	12.72	18.02
	68b	69b	70b	Mean	s_d (±)
Skin	3.04	2.48	2.67	2.59	0.42
Muscle ant. body	37.66	39.79	39.02	37.10	2.77
Muscle post. body	3.03	3.58	4.04	2.94	0.62
Total muscle	40.69	43.37	43.06	40.04	3.00
Diaphragm	0.94	1.22	0.89	0.97	0.24
Interscap. B.A.T.	7.40	6.98	8.57	9.60	1.99
Other B.A.T.	6.12	5.71	7.30	7.99	1.77
Total B.A.T.	13.52	12.69	15.87	17.59	3.58
Liver	1.73	1.78	1.29	1.80	0.61
Kidneys	0.61	0.87	0.66	0.70	0.10
Stomach	0.36	0.27	0.36	0.38	0.12
Intestine	0.97	0.47	0.68	0.83	0.25
Myocardium	5.11	5.56	5.37	5.78	0.68
Blood	13.94	14.81	14.13	13.68	1.83
W.A.T.	1.44	2.05	0.75	1.13	0.49
Carcass	17.64	14.42	14.27	14.51	2.53

Table 2 (continued)

	Group B				
	Subgroup 10: sacrificed at HR = 600 beats/min (arousal)				
	71b	72b	73b	74b	75b
Skin	3.95	4.79	4.90	3.55	3.90
Muscle ant. body	39.11	41.77	36.84	38.94	37.30
Muscle post. body	4.98	4.95	3.71	3.83	4.34
Total muscle	44.09	46.72	40.55	42.77	41.64
Diaphragm	0.68	1.15	0.73	0.67	0.86
Interscap. B.A.T.	6.09	6.74	7.98	7.58	7.42
Other B.A.T.	5.09	6.59	5.58	5.23	6.58
Total B.A.T.	11.18	13.33	13.56	12.81	14.00
Liver	3.10	1.46	2.41	1.81	2.44
Kidneys	0.53	0.35	0.48	0.30	0.33
Stomach	0.65	0.32	0.36	0.23	0.22
Intestine	0.94	0.55	0.52	0.49	0.39
Myocardium	4.87	5.49	4.59	4.43	5.40
Blood	12.08	8.95	13.79	12.77	12.66
W.A.T.	1.89	1.23	1.46	1.69	1.86
Carcass	16.00	15.67	16.62	18.49	16.31
	76b	77b	78b	Mean	s_d (±)
Skin	3.88	4.28	3.70	4.12	0.50
Muscle ant. body	37.64	37.60	41.90	38.89	1.98
Muscle post. body	3.90	5.21	4.20	4.39	0.60
Total muscle	41.54	42.81	46.10	43.28	2.21
Diaphragm	0.81	0.85	0.99	0.84	0.16
Interscap. B.A.T.	8.47	6.97	6.07	7.16	0.86
Other B.A.T.	6.51	5.22	5.14	5.74	0.69
Total B.A.T.	14.98	12.19	11.21	12.91	1.34
Liver	1.33	1.82	1.02	1.92	0.69
Kidneys	0.53	0.37	0.36	0.41	0.09
Stomach	0.40	0.53	0.31	0.38	0.16
Intestine	0.36	0.70	0.71	0.58	0.19
Myocardium	4.28	4.70	4.79	4.82	0.43
Blood	13.15	13.87	13.32	12.57	1.60
W.A.T.	2.55	2.28	1.12	1.76	0.49
Carcass	16.16	15.60	16.36	16.40	0.91

Table 2 (continued)

	Group B				
	Subgroup 11: sacrificed at HR = 800 beats/min (arousal)				
	79b	80b	81b	82b	83b
Skin	3.56	2.84	3.04	2.64	4.17
Muscle ant. body	39.00	41.86	37.15	35.29	43.52
Muscle post. body	5.24	7.39	4.89	8.77	9.26
Total muscle	44.24	49.25	42.04	44.06	52.78
Diaphragm	0.88	0.60	0.90	1.24	0.72
Interscap. B.A.T.	4.77	4.60	6.75	6.19	3.13
Other B.A.T.	4.44	3.54	4.78	6.15	2.70
Total B.A.T.	9.21	8.14	11.53	12.34	5.83
Liver	2.67	2.27	2.90	2.65	2.26
Kidneys	1.39	0.65	2.37	0.91	0.50
Stomach	0.34	0.33	0.65	0.40	0.38
Intestine	0.90	1.48	2.55	1.02	1.05
Myocardium	5.01	4.25	4.43	5.35	3.95
Blood	13.06	11.12	10.28	9.88	9.51
W.A.T.	1.79	1.79	2.59	1.83	2.63
Carcass	16.96	17.30	16.72	17.69	16.22
	84b	85b	86b	Mean	s_d (±)
Skin	3.36	3.68	3.15	3.31	0.49
Muscle ant. body	39.33	40.26	38.93	39.42	2.57
Muscle post. body	7.21	8.46	6.49	7.21	1.60
Total muscle	46.54	48.72	45.42	46.63	3.46
Diaphragm	0.96	1.22	1.12	0.96	0.23
Interscap. B.A.T.	4.98	3.44	6.10	5.00	1.30
Other B.A.T.	4.94	2.97	5.87	4.42	1.27
Total B.A.T.	9.92	6.41	11.97	9.42	2.49
Liver	3.06	1.70	2.29	2.48	0.43
Kidneys	2.52	0.50	0.85	1.21	0.81
Stomach	0.65	0.80	0.75	0.54	0.19
Intestine	3.41	1.08	1.55	1.63	0.89
Myocardium	5.48	4.89	4.75	4.76	0.53
Blood	10.38	10.91	11.10	10.78	1.09
W.A.T.	1.53	2.32	1.83	2.22	
Carcass	12.19	17.76	15.23	16.26	1.84

Table 2 (continued)

	Group B				
	Subgroup 12: sacrificed at HR = 480 beats/min (post-arousal; resting)				
	87b	88b	89b	90b	91b
Skin	4.83	6.19	7.26	7.08	6.27
Muscle ant. body	20.37	16.14	18.60	20.76	21.01
Muscle post. body	8.24	8.94	6.74	12.75	12.75
Total muscle	28.61	25.08	25.34	33.51	33.76
Diaphragm	0.67	1.37	0.72	0.76	0.88
Interscap. B.A.T.	6.77	6.38	6.38	3.22	4.16
Other B.A.T.	4.61	4.60	4.27	3.62	3.54
Total B.A.T.	11.38	10.98	10.65	6.84	7.70
Liver	3.92	4.06	4.46	3.66	3.10
Kidneys	5.94	4.71	4.47	4.29	3.86
Stomach	1.02	1.46	0.94	0.71	0.82
Intestine	6.38	3.68	3.59	3.14	3.28
Myocardium	3.42	3.01	3.46	4.00	3.57
Blood	14.19	14.74	15.65	14.62	14.06
W.A.T.	4.53	5.51	4.99	4.13	4.63
Carcass	15.12	19.22	18.46	17.26	18.07
	92b	93b	94b	Mean	s_d (±)
Skin	6.52	6.88	6.33	6.42	0.75
Muscle ant. body	24.31	24.04	21.71	20.87	2.68
Muscle post. body	9.46	12.25	9.23	10.04	2.26
Total muscle	33.77	36.29	30.94	30.91	4.18
Diaphragm	1.02	0.78	0.67	0.86	0.24
Interscap. B.A.T.	4.34	3.90	5.57	5.09	1.35
Other B.A.T.	4.37	3.17	5.12	4.16	0.66
Total B.A.T.	8.71	7.07	10.69	9.25	1.88
Liver	3.81	3.81	4.07	3.86	0.39
Kidneys	1.16	2.24	5.03	3.96	1.60
Stomach	0.92	1.23	1.11	1.03	0.18
Intestine	2.72	2.22	3.31	3.54	0.76
Myocardium	4.31	3.76	3.90	3.68	0.40
Blood	13.86	12.26	12.18	13.95	1.20
W.A.T.	0.52	3.52	3.31	3.89	1.54
Carcass	22.67	19.96	18.48	18.66	2.17

Table 3 (continued)

	Group C Subgroup 2: sacrificed at HR = 40 beats/min (arousal)					
	6c	7c	8c	9c	Mean	s_d (±)
Skin	5.02	5.62	6.14	4.94	5.43	0.56
Muscle ant. body	27.26	27.99	31.81	24.52	27.90	3.00
Muscle post. body	9.19	12.93	11.75	6.86	10.18	2.71
Total muscle	36.45	40.92	43.56	31.38	38.08	5.34
Diaphragm	1.36	1.22	1.03	1.06	1.17	0.15
Interscap. B.A.T.	3.22	3.01	1.88	5.20	3.33	1.38
Other B.A.T.	2.71	1.65	1.42	3.03	2.20	0.79
Total B.A.T.	5.93	4.66	3.30	8.23	5.53	2.10
Liver	2.81	3.39	2.96	3.46	3.16	0.32
Kidneys	1.39	1.79	0.78	2.18	1.54	0.60
Stomach	0.74	0.90	1.06	1.31	1.00	0.24
Intestine	6.22	1.54	2.83	6.85	4.36	2.58
Myocardium	4.74	2.86	2.78	3.47	3.46	0.91
Blood	15.56	14.44	12.16	12.98	13.79	1.51
W.A.T.	0.76	0.83	0.00	1.43	0.75	0.58
Carcass	18.99	21.85	23.40	22.69	21.73	1.93

Table 3 (continued)

	Group C Subgroup 3: sacrificed at HR = 80 beats/min (arousal)					
	10c	11c	12c	13c	Mean	s_d (±)
Skin	6.33	4.59	6.75	6.86	6.13	1.05
Muscle ant. body	35.89	38.21	34.73	27.64	34.12	4.55
Muscle post. body	9.75	13.16	13.84	8.42	11.29	2.62
Total muscle	45.64	51.37	48.57	36.06	45.41	6.66
Diaphragm	0.78	1.13	1.12	0.74	0.94	0.21
Interscap. B.A.T.	2.52	1.10	1.90	3.83	2.34	1.15
Other B.A.T.	2.36	1.35	1.76	2.50	1.99	0.54
Total B.A.T.	4.88	2.45	3.66	6.33	4.33	1.66
Liver	2.20	1.06	2.70	3.83	2.45	1.15
Kidneys	0.55	0.70	1.15	1.96	1.09	0.63
Stomach	1.02	0.59	1.87	0.95	1.11	0.54
Intestine	1.25	1.59	2.73	3.20	2.19	0.92
Myocardium	3.09	3.61	3.18	3.55	3.36	0.26
Blood	9.77	11.53	10.16	14.59	11.51	2.19
W.A.T.	0.80	1.44	1.23	1.20	1.17	0.27
Carcass	23.70	19.94	16.87	20.73	20.31	2.81

Table 3 (continued)

	Group C			
	Subgroup 4: sacrificed at HR = 120 beats/min (arousal)			
	14c	15c	16c	17c
Skin	3.23	6.65	7.25	6.49
Muscle ant. body	32.73	29.23	26.83	35.61
Muscle post. body	9.86	4.54	4.50	6.53
Total muscle	42.59	33.77	31.33	42.14
Diaphragm	0.79	0.87	0.79	0.91
Interscap. B.A.T.	5.16	6.68	5.72	2.44
Other B.A.T.	4.22	5.55	5.39	2.33
Total B.A.T.	9.38	12.23	11.11	4.77
Liver	3.52	4.34	3.40	3.02
Kidneys	0.65	0.60	0.75	1.06
Stomach	0.47	0.44	0.47	1.12
Intestine	0.76	0.90	0.92	1.55
Myocardium	5.09	5.99	4.50	4.73
Blood	14.24	14.21	17.08	14.44
W.A.T.	1.07	0.48	0.65	0.93
Carcass	18.20	19.52	21.77	18.85

	18c	Mean	s_d (±)
Skin	7.88	6.30	1.80
Muscle ant. body	27.34	30.35	3.74
Muscle post. body	7.08	6.50	2.21
Total muscle	34.42	36.85	5.17
Diaphragm	1.19	0.91	0.16
Interscap. B.A.T.	5.31	5.06	1.58
Other B.A.T.	4.30	4.34	1.29
Total B.A.T.	9.61	9.42	2.85
Liver	2.27	3.31	0.75
Kidneys	1.19	0.85	0.26
Stomach	0.80	0.66	0.30
Intestine	1.53	1.13	0.38
Myocardium	6.10	5.28	0.73
Blood	13.60	14.71	1.36
W.A.T.	1.26	0.88	0.31
Carcass	20.16	19.70	1.37

Table 3 (continued)

	Group C					
	Subgroup 5: sacrificed at HR = 180 beats/min (arousal)					
	19c	20c	21c	22c	Mean	s_d (±)
Skin	4.26	6.93	3.80	5.20	5.05	1.38
Muscle ant. body	39.68	33.69	40.53	35.91	37.45	3.21
Muscle post. body	11.63	10.01	11.11	7.77	10.13	1.71
Total muscle	51.31	43.70	51.64	43.68	47.58	4.50
Diaphragm	0.80	0.69	0.75	1.47	0.92	0.36
Interscap. B.A.T.	3.77	3.26	4.07	5.20	4.08	0.82
Other B.A.T.	3.55	3.06	4.21	4.61	3.86	0.69
Total B.A.T.	7.32	6.32	8.28	9.81	7.93	1.49
Liver	1.72	1.45	1.02	1.17	1.34	0.31
Kidneys	0.68	1.10	1.06	0.68	0.88	0.23
Stomach	0.37	0.43	0.58	0.44	0.46	0.09
Intestine	0.77	0.76	0.89	0.60	0.76	0.12
Myocardium	4.33	2.56	3.81	4.56	3.82	0.89
Blood	8.22	11.35	10.59	10.88	10.26	1.40
W.A.T.	1.34	0.69	0.76	0.60	0.85	0.33
Carcass	18.90	24.03	16.82	20.91	20.16	3.07

Table 3 (continued)

	Group C			
	Subgroup 6: sacrificed at HR = 240 beats/min (arousal)			
	23c	24c	25c	26c
Skin	4.39	2.84	2.92	5.50
Muscle ant. body	37.36	38.07	38.63	37.70
Muscle post. body	8.58	7.01	7.06	8.02
Total muscle	45.94	45.08	45.69	45.72
Diaphragm	1.11	1.01	1.05	0.87
Interscap. B.A.T.	3.50	6.27	6.34	4.45
Other B.A.T.	2.96	6.02	5.99	3.66
Total B.A.T.	6.46	12.29	12.33	8.11
Liver	1.37	1.21	1.25	1.91
Kidneys	0.32	0.26	0.27	0.81
Stomach	0.47	1.13	0.66	0.82
Intestine	0.58	0.63	1.13	0.89
Myocardium	5.39	4.53	4.53	4.35
Blood	12.66	14.68	13.66	11.00
W.A.T.	0.44	0.65	0.65	1.15
Carcass	20.87	15.69	15.83	18.86
	27c	Mean		s_d (±)
Skin	6.06	4.34		1.46
Muscle ant. body	36.96	37.74		0.64
Muscle post. body	6.74	7.48		0.78
Total muscle	43.70	45.22		0.93
Diaphragm	0.92	0.99		0.10
Interscap. B.A.T.	3.23	4.76		1.48
Other B.A.T.	2.59	4.24		1.65
Total B.A.T.	5.82	9.00		3.13
Liver	2.28	1.60		0.47
Kidneys	1.60	0.65		0.58
Stomach	0.90	0.77		0.25
Intestine	2.73	1.19		0.89
Myocardium	5.65	4.89		0.59
Blood	10.70	12.54		1.70
W.A.T.	1.80	0.94		0.55
Carcass	17.83	17.82		2.17

Table 3 (continued)

	Group C Subgroup 8: sacrificed at HR = 360 beats/min (arousal)					
	28c	29c	30c	31c	Mean	s_d (±)
Skin	6.74	3.05	3.03	6.73	4.89	2.13
Muscle ant. body	40.74	37.28	37.22	37.20	38.11	1.75
Muscle post. body	4.97	6.45	6.39	5.29	5.78	0.76
Total muscle	45.71	43.73	43.61	42.49	43.89	1.34
Diaphragm	0.90	0.86	0.84	0.81	0.85	0.04
Interscap. B.A.T.	4.65	7.11	7.15	4.40	5.83	1.51
Other B.A.T.	3.66	6.00	5.97	3.64	4.82	1.35
Total B.A.T.	8.31	13.11	13.12	8.04	10.64	2.85
Liver	1.08	1.66	1.66	1.25	1.41	0.29
Kidneys	0.54	0.37	0.42	1.66	0.75	0.61
Stomach	0.30	0.47	0.47	0.58	0.46	0.12
Intestine	0.47	0.97	0.97	2.12	1.13	0.70
Myocardium	4.53	5.47	5.48	4.61	5.02	0.52
Blood	9.15	12.44	12.35	12.51	11.61	1.64
W.A.T.	2.10	0.89	0.89	1.57	1.36	0.59
Carcass	20.18	16.99	17.15	17.62	17.98	1.48

Table 3 (continued)

	Group C Subgroup 9: sacrificed at HR = 480 beats/min (arousal)			
	32c	33c	34c	35c
Skin	6.47	7.39	7.76	5.99
Muscle ant. body	43.19	34.92	37.01	38.44
Muscle post. body	4.40	5.41	7.24	3.64
Total muscle	47.59	40.33	44.25	42.08
Diaphragm	0.91	1.14	0.97	0.91
Interscap. B.A.T.	3.92	6.17	3.75	3.43
Other B.A.T.	2.49	5.64	2.71	2.88
Total B.A.T.	6.41	11.81	6.46	6.31
Liver	0.89	1.69	1.01	1.40
Kidneys	0.24	1.39	0.56	1.97
Stomach	0.54	0.34	1.00	0.73
Intestine	0.54	0.81	0.76	2.50
Myocardium	4.80	6.77	5.95	3.16
Blood	10.87	8.90	9.07	13.52
W.A.T.	0.54	0.97	0.54	1.99
Carcass	20.20	18.46	21.67	19.43

	36c	Mean	s_d (±)
Skin	5.75	6.67	0.87
Muscle ant. body	41.86	39.08	3.41
Muscle post. body	3.41	4.82	1.56
Total muscle	45.27	43.90	2.81
Diaphragm	0.75	0.94	0.14
Interscap. B.A.T.	4.32	4.31	1.08
Other B.A.T.	2.94	3.33	1.30
Total B.A.T.	7.26	7.65	2.36
Liver	2.50	1.50	0.64
Kidneys	1.47	1.12	0.71
Stomach	0.75	0.67	0.25
Intestine	2.80	1.48	1.08
Myocardium	4.47	5.03	1.39
Blood	11.96	10.86	1.96
W.A.T.	0.39	0.88	0.65
Carcass	16.63	19.28	1.89

Table 3 (continued)

	Group C Subgroup 10: sacrificed at HR = 600 beats/min (arousal)					
	37c	38c	39c	40c	Mean	s_d (±)
Skin	3.77	2.99	5.21	5.53	4.38	1.20
Muscle ant. body	35.93	44.42	43.26	41.12	41.18	3.75
Muscle post. body	3.53	3.80	3.35	4.28	3.74	0.40
Total muscle	39.46	48.22	46.61	45.40	44.92	3.82
Diaphragm	0.84	0.72	0.64	0.73	0.73	0.08
Interscap. B.A.T.	5.16	4.45	5.25	5.91	5.19	0.60
Other B.A.T.	3.89	4.03	3.83	5.03	4.20	0.56
Total B.A.T.	9.05	8.48	9.08	10.94	9.39	1.07
Liver	5.09	2.19	2.44	3.35	3.27	1.31
Kidneys	1.61	1.72	1.42	1.46	1.55	0.14
Stomach	0.90	0.67	0.56	0.62	0.69	0.15
Intestine	2.26	1.34	1.71	1.47	1.69	0.41
Myocardium	4.72	5.63	4.47	4.03	4.71	0.67
Blood	11.51	9.70	9.74	11.19	10.54	0.95
W.A.T.	1.62	1.06	1.28	0.24	1.05	0.59
Carcass	19.17	17.27	16.85	15.03	17.08	1.70

Table 3 (continued)

	Group C			
	Subgroup 11: sacrificed at HR = 740 beats/min (arousal)			
	41c	42c	43c	44c
Skin	5.17	5.35	3.28	5.27
Muscle ant. body	35.87	42.76	43.45	41.62
Muscle post. body	7.16	9.69	8.48	9.57
Total muscle	43.03	52.45	51.93	51.19
Diaphragm	0.84	0.65	1.03	0.63
Interscap. B.A.T.	2.36	2.17	3.03	2.11
Other B.A.T.	2.41	1.98	2.46	1.93
Total B.A.T.	4.77	4.15	5.49	4.04
Liver	4.74	3.66	2.41	3.47
Kidneys	2.83	1.45	0.39	1.39
Stomach	1.81	1.36	1.11	1.32
Intestine	5.79	2.77	0.62	2.69
Myocardium	3.32	4.13	5.17	3.99
Blood	11.76	8.54	10.63	10.70
W.A.T.	0.79	0.56	1.17	0.53
Carcass	15.16	14.93	16.78	14.76

	45c	Mean	s_d (±)
Skin	3.79	4.57	0.97
Muscle ant. body	43.06	41.35	3.14
Muscle post. body	8.50	8.68	0.76
Total muscle	51.56	50.03	3.94
Diaphragm	0.76	0.78	0.16
Interscap. B.A.T.	3.43	2.62	0.58
Other B.A.T.	2.34	2.22	0.25
Total B.A.T.	5.77	4.84	0.76
Liver	2.21	3.30	1.03
Kidneys	3.90	1.99	1.38
Stomach	0.91	1.30	0.34
Intestine	3.21	3.02	1.85
Myocardium	5.15	4.35	0.80
Blood	9.13	10.15	1.30
W.A.T.	2.20	1.05	0.69
Carcass	11.43	14.61	1.95

Table 3 (continued)

	Group C Subgroup 12: sacrificed at HR = 480 beats/min (post-arousal; resting)					
	46c	47c	48c	49c	Mean	s_d (±)
Skin	6.43	5.88	4.67	6.54	5.88	0.86
Muscle ant. body	30.91	30.14	30.28	31.34	30.67	0.56
Muscle post. body	8.77	9.89	10.40	9.19	9.56	0.72
Total muscle	39.68	40.03	40.68	40.53	40.23	0.46
Diaphragm	0.96	1.08	1.21	1.15	1.10	0.11
Interscap. B.A.T.	2.21	0.97	0.57	2.32	1.52	0.88
Other B.A.T.	1.70	0.94	0.57	1.49	1.18	0.52
Total B.A.T.	3.91	1.91	1.14	3.81	2.70	1.40
Liver	4.35	7.64	4.41	4.33	5.18	1.64
Kidneys	5.00	6.65	4.90	5.59	5.54	0.80
Stomach	0.92	1.80	1.08	1.38	1.30	0.40
Intestine	5.68	6.05	6.25	4.59	5.64	0.74
Myocardium	4.02	2.84	4.52	3.91	3.82	0.71
Blood	9.59	8.59	12.38	9.93	10.12	1.61
W.A.T.	0.00	1.31	2.65	1.41	1.79	0.75
Carcass	19.46	16.24	16.09	16.83	17.15	1.57

APPENDIX 5

TEMPERATURES OF *E. FUSCUS* AT DIFFERENT HEART RATES

Table 1. Interscapular brown adipose tissue temperatures of *E.*

	HEART RATES (BEATS/									
	40	80	120	180	240	300	360	400	440	480
Animal	Brown adipose									
1	6.5	9.5	13.0	17.0	20.0	22.0	23.0	27.0	30.0	33.0
2	6.0	8.5	11.5	15.5	18.5	21.0	22.5	26.0	27.0	28.0
3	6.5	9.0	12.5	16.0	19.0	22.0	25.0	27.0	29.0	30.0
4	6.5	9.5	13.0	16.5	19.0	22.0	24.0	27.0	28.0	29.0
5	6.0	9.0	13.0	16.0	19.5	22.5	25.0	27.0	28.0	30.0
6	6.5	10.0	14.0	18.0	20.0	22.0	24.0	27.0	29.0	30.0
7	6.0	9.0	13.0	17.0	20.0	23.0	25.5	28.0	29.5	30.5
8	6.0	9.0	13.0	17.0	19.5	22.0	25.0	26.5	27.5	29.0
9	6.5	9.0	13.0	16.5	19.5	22.0	25.0	28.0	29.0	30.5
10	6.0	9.0	12.0	15.5	18.5	22.0	24.0	25.0	26.0	27.0
11	6.0	10.5	13.0	17.5	20.0	22.5	25.5	27.0	29.0	30.5
12	6.5	10.0	14.0	18.0	22.0	24.5	26.0	28.5	31.5	33.0
13	6.0	7.5	12.0	16.5	19.5	22.5	25.0	27.0	29.0	30.5
14	6.5	9.5	12.5	16.0	19.0	22.0	24.5	26.0	27.5	29.0
15	6.0	8.5	12.0	16.0	18.0	22.0	24.0	25.0	26.0	28.0
16	6.0	8.5	11.0	14.0	17.5	20.0	22.0	24.0	25.5	28.0
17	6.0	9.0	12.0	15.5	17.5	22.0	24.0	25.0	26.0	27.0
18	6.0	7.5	12.0	15.0	19.0	22.0	24.5	25.0	26.0	28.0
19	6.5	9.5	13.5	17.5	22.0	24.5	27.0	29.0	31.0	33.0
20	6.0	8.0	12.0	16.0	19.5	23.0	24.5	29.0	30.0	32.0
Mean	6.2	9.0	12.6	16.4	19.4	22.3	24.5	26.7	28.2	29.8
s_d (±)	0.2	0.8	0.8	1.0	1.2	1.0	1.2	1.4	1.7	1.9

DURING AROUSAL FROM HIBERNATION IN THE WINTER (T_a = 5 C)

fuscus at different heart rates during arousal from hibernation

MINUTE) DURING AROUSAL					2-minute time intervals					
520	580	640	700	760	800	800	800	800	760	760
tissue temperatures (°C)										
34.0	35.0	36.0	37.0	37.5	38.0	38.5	38.5	38.5	38.5	38.5
29.5	30.5	32.0	34.0	36.0	37.5	38.5	39.0	39.0	39.0	39.0
32.0	33.0	35.0	36.0	37.0	39.0	40.0	40.0	40.0	40.0	40.0
30.0	31.5	33.0	36.5	37.5	38.0	38.0	38.0	38.0	38.0	38.0
32.0	33.0	35.0	36.0	37.0	39.0	39.5	40.0	40.0	40.0	40.0
32.5	34.0	35.0	36.0	37.0	38.5	39.0	39.0	39.0	39.0	39.0
32.0	32.5	34.0	36.0	36.5	38.0	38.5	39.0	39.0	39.0	39.0
30.0	32.5	34.0	35.0	36.5	37.5	38.0	38.5	38.5	38.5	38.5
31.5	33.0	35.0	37.0	38.5	39.0	39.0	38.0	38.0	38.0	38.0
28.0	31.0	34.0	35.0	37.0	38.0	39.0	40.0	40.0	40.0	40.0
31.5	32.5	35.0	37.0	39.0	40.0	38.5	39.0	39.0	39.0	39.0
34.5	35.5	36.5	37.5	38.0	39.0	40.0	40.0	40.0	40.0	40.0
31.5	33.0	34.0	36.0	37.0	37.5	38.0	38.0	38.0	38.0	38.0
30.0	31.5	32.5	34.5	36.0	37.0	38.0	38.5	38.5	38.5	38.5
29.0	30.0	32.0	35.0	36.0	37.0	38.0	38.0	38.0	38.0	38.0
28.5	30.5	31.5	33.5	35.0	37.0	38.0	38.5	38.5	38.5	38.5
29.0	31.0	34.0	35.0	37.0	38.0	39.0	39.5	39.5	39.5	39.5
29.0	30.5	33.5	33.5	35.0	37.0	38.0	39.0	39.0	39.0	39.0
34.0	36.0	37.0	38.0	38.5	39.0	39.5	40.0	40.0	40.0	40.0
33.0	34.5	35.0	36.0	37.0	38.0	38.5	39.0	39.0	39.0	39.0
31.1	32.5	34.2	35.7	37.0	38.1	38.7	39.0	39.0	39.0	39.0
2.0	1.8	1.5	1.3	1.1	0.9	0.7	0.7	0.7	0.7	0.7

Table 2. Anterior skeletal muscle temperatures of *E. fuscus*

	HEART RATES (BEATS/									
	40	80	120	180	240	300	360	400	440	480
Animal	Anterior skeletal									
1	6.0	9.0	11.0	15.0	18.0	19.5	21.0	23.5	26.0	29.0
2	6.0	8.5	10.5	13.0	15.0	16.5	18.0	20.0	21.0	22.0
3	6.0	8.5	10.0	12.5	15.0	17.0	19.5	21.0	22.0	23.5
4	6.0	7.0	9.0	11.0	13.0	15.5	17.5	19.0	20.0	21.5
5	6.5	8.0	9.5	12.0	14.0	16.0	18.5	20.0	21.0	23.5
6	6.5	8.5	11.0	14.0	16.0	17.0	18.5	21.0	23.0	24.5
7	6.0	7.5	10.5	13.5	16.5	18.5	20.5	23.0	24.0	25.0
8	6.0	7.5	9.5	13.0	15.0	16.5	18.5	20.0	21.5	22.5
9	6.5	9.5	10.0	12.0	14.5	16.0	19.5	21.0	22.0	23.5
10	6.0	9.0	10.0	12.0	14.0	16.5	18.0	19.0	19.5	20.0
11	6.0	9.5	10.0	13.0	14.5	16.0	17.5	19.5	21.5	23.5
12	6.0	8.0	9.5	12.0	15.0	16.5	17.5	20.0	23.0	25.5
13	6.5	8.0	9.0	11.5	13.5	15.0	17.0	18.0	19.5	21.5
14	6.5	9.0	10.0	12.0	14.0	15.0	16.0	19.0	22.0	23.5
15	6.0	8.5	10.5	13.0	15.0	17.0	19.0	19.5	21.0	21.5
16	6.0	8.5	9.0	11.5	13.0	15.0	16.0	17.0	19.0	20.0
17	6.5	9.0	10.0	11.0	14.5	16.5	17.5	18.5	19.5	20.0
18	6.0	7.0	10.0	12.0	16.0	18.0	20.0	22.5	23.0	23.5
19	6.5	9.0	11.0	14.0	17.5	20.0	22.0	24.0	26.5	28.5
20	6.0	8.0	10.0	12.0	15.0	17.0	19.0	23.0	25.5	26.5
Mean	6.2	8.4	10.0	12.5	15.0	16.8	18.6	20.4	22.0	23.4
s_d (±)	0.2	0.7	0.6	1.1	1.3	1.4	1.6	1.9	2.2	2.6

at different heart rates during arousal from hibernation

MINUTE) DURING AROUSAL					2-minute time intervals						
520	580	640	700	760	800	800	800	800	760	760	740
muscle temperatures (°C)											
30.0	31.0	33.0	34.0	35.0	35.5	37.5	38.0	38.0	38.0	38.0	38.0
23.0	24.0	26.0	28.0	30.0	33.0	35.0	37.0	37.0	37.0	37.0	37.0
25.0	26.0	27.0	30.0	33.0	35.0	36.0	37.0	37.0	37.0	37.0	37.0
23.0	24.0	26.0	29.0	30.0	32.0	33.5	35.0	36.0	37.0	37.0	37.0
25.0	25.5	27.5	29.0	30.0	33.0	35.0	36.5	37.0	37.0	37.0	37.0
26.0	28.5	29.0	30.5	32.0	33.5	35.0	35.5	36.0	36.0	36.0	36.0
26.0	27.0	28.0	30.0	31.0	33.0	35.0	36.5	37.5	37.5	37.5	37.5
23.5	25.0	26.0	28.5	30.0	32.0	34.0	36.0	37.0	37.0	37.0	37.0
23.5	26.0	27.5	29.5	32.0	33.5	35.0	35.5	35.5	35.5	35.5	35.5
22.5	25.0	27.0	28.5	30.5	32.0	34.0	36.0	36.5	36.5	36.5	36.5
25.0	27.0	29.5	31.5	33.0	34.5	35.5	36.0	36.5	36.5	36.5	36.5
27.0	29.0	30.0	32.0	34.0	35.0	35.5	35.5	35.5	35.5	35.5	35.5
23.0	27.0	29.0	30.5	31.5	33.0	34.5	35.5	36.0	36.0	36.0	36.0
25.0	27.0	29.0	31.0	33.0	34.0	35.5	36.0	36.0	36.0	36.0	36.0
22.5	25.0	27.0	29.0	30.5	32.0	34.0	35.0	35.0	35.0	35.0	35.0
22.0	24.0	27.0	39.0	30.0	32.0	34.5	35.0	35.0	35.0	35.0	35.0
22.5	24.5	26.5	30.0	32.0	33.0	34.0	34.5	35.0	35.0	35.0	35.0
24.5	26.5	28.5	30.0	32.0	33.0	34.0	35.0	35.0	35.0	35.0	35.0
29.0	30.0	31.0	32.0	33.0	34.5	35.5	36.0	36.0	35.0	35.0	35.0
28.0	29.0	30.0	31.0	33.0	34.0	35.0	35.5	35.5	35.5	35.5	35.5
24.8	26.6	28.2	30.1	31.2	33.4	34.9	35.9	36.2	36.2	36.2	36.2
2.3	2.1	1.9	2.4	1.2	1.1	0.9	0.8	0.9	0.9	0.9	0.9

Table 3. Posterior skeletal muscle temperatures of *E. fuscus*

	HEART RATES (BEATS/									
	40	80	120	180	240	300	360	400	440	480
Animal	Posterior skeletal									
1	7.0	10.0	12.0	13.5	14.5	16.0	17.0	17.5	19.0	20.0
2	8.0	10.0	13.0	14.5	15.5	16.0	16.5	17.0	17.0	17.5
3	8.0	8.5	10.0	11.0	12.0	13.0	13.5	14.0	15.0	16.0
4	7.0	8.0	9.0	10.0	11.5	12.0	13.0	10.0	10.5	12.0
5	7.5	9.0	9.5	10.5	11.0	12.0	13.0	13.5	14.0	15.0
6	7.0	8.0	8.5	9.0	9.0	9.5	9.5	12.0	14.0	15.0
7	7.5	9.5	11.0	12.0	13.0	14.0	15.0	15.0	15.0	15.5
8	8.0	9.0	10.5	11.0	11.5	13.0	13.0	13.0	13.0	13.5
9	8.0	10.0	10.5	11.0	11.0	11.0	11.5	12.0	12.0	12.5
10	8.0	9.0	10.5	12.0	13.5	14.0	14.5	15.0	15.5	15.5
11	8.0	10.0	11.5	13.5	14.5	15.5	17.0	18.0	18.5	19.0
12	8.0	10.0	10.5	11.0	12.5	13.0	13.0	13.5	15.0	16.0
13	7.5	9.0	9.5	10.5	11.0	12.0	12.5	13.0	14.0	15.0
14	7.5	9.0	9.5	10.5	11.0	11.0	12.0	12.5	13.0	13.0
15	7.5	9.0	10.0	11.0	12.0	13.0	14.0	14.0	14.5	15.0
16	7.0	7.5	8.5	9.0	10.0	10.0	10.5	10.5	11.0	11.0
17	7.0	9.5	10.0	11.5	13.0	14.0	14.5	15.0	15.0	15.5
18	6.0	7.0	9.5	11.5	13.0	14.0	15.0	16.0	16.5	17.0
19	8.0	9.5	10.0	12.0	13.5	14.5	15.0	16.0	19.0	21.0
20	6.5	7.5	9.0	10.0	12.0	12.5	14.5	16.5	18.0	19.5
Mean	7.4	9.0	10.1	11.2	12.2	13.0	13.7	14.2	15.0	15.7
s_d (±)	0.6	0.9	1.3	2.0	1.6	1.8	2.0	2.2	1.9	2.7

at different heart rates during arousal from hibernation

MINUTE) DURING AROUSAL					2-minute time intervals						
520	580	640	700	760	800	800	800	800	760	760	740
muscle temperatures (°C)											
21.0	23.0	26.0	28.0	29.0	31.0	33.0	35.0	36.0	36.0	36.0	36.0
18.0	18.5	19.5	21.0	23.0	27.0	29.0	31.0	32.5	33.5	34.5	35.0
17.0	18.0	19.0	23.0	28.0	33.0	35.0	36.0	36.5	36.5	36.5	36.5
13.0	16.0	21.0	23.0	27.0	29.0	31.0	32.0	33.5	34.0	34.0	34.0
15.0	16.0	17.0	18.0	23.0	26.0	29.5	31.0	32.5	33.0	33.0	33.0
15.5	16.5	18.0	22.5	26.0	29.0	31.0	32.0	33.0	33.0	33.0	33.0
16.5	16.5	17.0	19.0	20.0	25.0	27.0	28.0	31.5	33.0	34.0	34.0
14.0	14.5	15.5	18.0	19.0	23.5	27.0	30.0	32.0	33.5	34.5	35.0
13.0	14.0	17.5	20.0	24.0	28.0	30.0	32.0	33.0	33.5	34.0	34.0
16.0	18.0	20.0	22.0	24.5	27.0	29.0	32.0	33.0	34.0	35.0	36.0
20.0	22.0	24.0	26.5	29.5	31.0	33.0	34.5	35.5	36.0	36.0	36.0
16.5	16.5	17.0	20.0	24.0	26.0	28.0	30.0	31.5	32.0	33.0	33.0
17.0	18.0	18.5	20.0	23.0	27.0	30.0	32.0	33.0	33.5	34.0	34.0
14.0	15.0	16.0	18.0	21.0	23.0	27.0	29.0	30.0	32.	32.0	32.0
15.5	16.0	17.0	18.5	19.5	25.0	27.0	29.0	30.0	32.0	33.0	33.0
12.0	13.0	14.0	17.0	21.0	26.0	29.0	31.0	23.5	33.0	33.0	33.0
16.5	17.5	20.0	21.5	24.0	26.0	29.0	31.0	33.0	34.0	35.0	35.0
18.5	20.0	22.0	24.0	25.5	27.5	29.0	30.5	32.5	33.5	34.0	34.0
23.0	25.0	26.0	28.0	29.0	31.0	33.0	34.0	35.0	36.0	36.5	36.5
20.0	21.5	22.5	23.0	24.5	27.5	29.0	30.0	31.0	32.0	33.0	33.0
16.6	17.7	19.4	21.6	24.2	27.4	29.8	31.5	32.4	33.7	34.2	34.3
2.9	3.1	3.4	3.3	2.5	2.6	2.3	2.1	2.7	1.4	1.3	1.4

Table 4. Colonic temperatures of *E. fuscus* at

	HEART RATES (BEATS/									
	40	80	120	180	240	300	360	400	440	480
Animal	Colonic									
1	8.0	13.0	14.5	15.0	15.5	15.5	16.0	16.0	16.0	16.5
2	7.0	10.0	12.0	13.5	14.5	15.0	15.5	16.0	16.5	16.5
3	6.5	9.0	10.5	11.5	12.5	13.0	13.5	13.5	14.0	14.5
4	7.0	8.0	9.0	9.5	10.0	10.5	11.0	11.5	12.0	13.0
5	6.5	9.5	10.5	11.0	11.5	12.0	12.5	13.0	13.0	14.0
6	7.0	10.0	9.5	9.5	10.0	10.0	10.0	10.0	10.0	10.5
7	6.0	10.0	11.5	12.5	13.0	14.0	15.0	15.0	15.0	15.0
8	8.0	11.0	11.5	12.0	12.0	12.5	12.5	13.0	13.0	13.5
9	7.0	10.0	10.0	11.0	11.0	11.0	11.5	12.0	12.0	12.0
10	7.0	10.0	12.0	13.5	14.0	14.0	15.0	15.0	15.0	15.0
11	7.5	11.0	13.0	14.0	15.0	15.5	16.5	17.5	18.0	19.0
12	5.5	10.0	12.0	13.0	14.0	14.0	14.5	14.5	15.5	16.0
13	6.0	9.0	10.0	10.5	11.0	11.0	11.0	11.5	12.0	12.0
14	7.0	11.0	13.5	14.0	14.5	14.5	14.5	14.5	14.5	14.5
15	6.5	8.0	8.5	10.0	11.0	12.0	13.0	13.0	14.0	14.0
16	5.0	7.0	8.0	8.5	9.0	10.0	10.0	10.0	10.5	11.0
17	7.0	10.0	11.5	13.5	14.0	14.5	15.0	15.0	15.0	15.0
18	6.5	8.0	8.5	9.5	10.0	10.0	10.0	10.0	10.0	11.0
19	6.0	9.5	11.5	13.0	13.5	14.5	15.0	16.0	16.0	16.0
20	7.5	10.0	10.5	11.0	11.0	11.5	12.0	13.5	14.0	15.0
Mean	6.7	9.7	10.9	11.8	12.4	12.8	13.2	13.5	13.8	14.2
s_d (±)	0.8	1.3	1.7	1.8	1.9	1.9	2.1	2.2	2.2	2.2

different heart rates during arousal from hibernation

MINUTE) DURING AROUSAL					2-minute time intervals						
520	580	640	700	760	800	800	800	800	760	760	740
temperatures (°C)											
16.5	16.5	17.0	18.5	20.0	23.0	26.0	29.0	32.0	33.0	34.0	34.0
17.0	17.5	18.5	19.0	22.0	26.0	28.0	29.5	32.0	34.0	34.0	34.0
14.5	15.0	15.5	17.5	19.0	23.0	25.0	29.0	30.0	33.0	35.0	35.0
13.0	14.0	15.0	16.0	18.0	20.0	25.0	29.0	31.5	33.0	35.0	35.0
14.5	15.0	16.0	17.5	19.0	23.5	26.5	29.0	31.0	32.0	32.5	32.5
10.5	11.0	11.5	12.0	14.0	16.0	18.0	22.0	25.0	28.0	30.0	30.0
15.5	16.0	17.0	19.0	21.0	24.0	26.0	28.5	31.0	32.0	32.5	32.5
15.0	17.0	18.0	18.5	19.0	22.0	26.0	27.0	29.5	30.0	30.0	30.0
12.0	12.5	13.0	13.5	16.0	19.0	22.0	25.0	27.5	29.0	30.0	30.0
15.5	16.0	17.5	18.5	21.5	24.5	27.0	29.0	31.0	32.0	33.0	33.0
20.0	22.0	24.0	25.0	27.0	29.0	30.0	32.0	33.0	34.0	34.5	34.5
16.5	17.5	19.0	20.0	21.0	26.0	30.0	34.0	36.0	36.5	36.0	36.0
13.0	14.0	15.0	19.0	20.0	23.0	27.0	29.0	31.0	31.5	32.0	32.0
15.0	15.0	16.0	16.5	19.0	23.0	27.0	31.0	34.0	34.5	34.5	34.5
15.0	15.5	16.0	17.0	19.0	21.0	23.0	25.0	28.0	29.0	30.0	30.0
11.5	12.0	12.5	14.0	17.0	22.0	26.5	29.0	31.0	32.5	33.0	33.0
15.5	16.5	17.5	19.0	22.0	24.0	27.0	29.0	31.0	32.0	33.0	33.0
12.0	15.0	17.0	18.5	21.0	23.0	25.0	28.0	29.0	30.0	30.5	30.5
16.5	17.5	19.0	22.0	24.0	26.0	28.0	30.0	31.0	32.0	32.5	32.5
16.0	17.0	19.0	23.0	26.0	28.0	30.0	32.0	33.0	34.5	35.0	35.0
14.8	15.6	16.7	18.2	20.3	23.3	26.2	28.8	30.9	32.1	32.9	32.9
2.2	2.4	2.7	3.1	3.1	3.0	2.8	2.7	2.4	2.1	1.9	1.9

APPENDIX 6

STATISTICAL ANALYSIS. The Student-Newman-Keuls procedure for unequal sample sizes was used to measure differences among means. Arranged in order of largest to smallest, means not significantly different from each other at the 5 percent (———) and 1 percent (- - -) level of probability are joined by lines.

Table 1. Results from statistical analysis on percentages (%) of injected 86-Rb (Rubidium) per organ or tissue of *E. fuscus*, sacrificed during deep hibernation (DH), at various heart rates (HR) during the arousal from hibernation, and during post-arousal (PA) in the winter.

Skin	
HR	% 86-Rb
PA 480	6.42
DH 12	5.70
600	4.12
800	3.31
40	3.24
180	3.06
360	2.80
80	2.74
480	2.59
300	2.59
240	2.52
120	2.39

Muscle ant. body	
HR	% 86-Rb
800	39.42
600	38.89
480	37.10
360	36.48
240	34.78
120	34.72
40	34.28
300	33.14
180	32.88
80	29.35
DH 12	22.92
PA 480	20.87

Muscle post. body	
HR	% 86-Rb
PA 480	10.04
DH 12	9.98
40	9.53
800	7.21
80	7.15
120	6.63
300	4.97
180	4.61
600	4.39
360	4.26
240	4.04
480	2.94

Total muscle	
HR	% 86-Rb
800	46.63
40	43.81
600	43.28
120	41.34
360	40.72
480	40.04
240	38.81
300	38.11
180	37.49
80	36.50
DH 12	32.91
PA 480	30.91

Diaphragm	
HR	% 86-Rb
480	0.97
800	0.96
360	0.95
300	0.86
PA 480	0.86
600	0.84
240	0.82
180	0.76
40	0.75
120	0.72
80	0.72
DH 12	0.72

Interscap. B.A.T.	
HR	% 86-Rb
240	13.74
80	12.36
180	11.67
300	11.01
120	10.14
480	9.60
360	9.39
600	7.16
40	5.41
PA 480	5.09
800	5.00
DH 12	2.63

Table 1 (continued)

Myocardium	
HR	% 86-Rb
480	5.78
300	4.90
360	4.85
600	4.82
800	4.76
180	4.51
240	4.13
PA 480	3.68
120	3.33
80	2.83
DH 12	2.75
40	2.37

Blood	
HR	% 86-Rb
40	16.38
80	15.69
DH 12	15.24
PA 480	13.95
120	13.89
480	13.68
360	13.31
300	13.21
180	12.99
600	12.57
240	12.40
800	10.78

W.A.T.	
HR	% 86-Rb
DH 12	4.25
PA 480	3.89
800	2.22
40	1.96
300	1.84
80	1.82
600	1.76
120	1.62
180	1.55
240	1.50
360	1.34
480	1.13

Carcass	
HR	% 86-Rb
DH 12	20.54
PA 480	18.66
40	17.07
600	16.40
800	16.26
180	16.22
360	15.97
300	15.11
80	14.67
480	14.51
120	14.22
240	13.14

Table 2. Results from statistical analysis on percentages (%) of injected 86-Rb (Rubidium) per organ or tissue of *E. fuscus*, sacrificed during deep hibernation (DH), at various heart rates (HR) during the arousal from hibernation, and during post-arousal (PA) in the summer.

Skin	
HR	% 86-Rb
DH 12	6.98
480	6.67
120	6.30
80	6.13
PA 480	5.88
40	5.43
180	5.05
360	4.89
740	4.57
600	4.38
240	4.34

Muscle ant. body	
HR	% 86-Rb
740	41.35
600	41.18
480	39.08
360	38.11
240	37.74
180	37.45
80	34.12
PA 480	30.67
120	30.35
40	27.90
DH 12	22.24

Muscle post. body	
HR	% 86-Rb
80	11.29
40	10.18
180	10.13
PA 480	9.56
740	8.68
DH 12	8.11
240	7.48
120	6.50
360	5.78
480	4.82
600	3.74

Total muscle	
HR	% 86-Rb
740	50.03
180	47.58
80	45.41
240	45.22
600	44.92
480	43.90
360	43.89
PA 480	40.23
40	38.08
120	36.85
DH 12	30.35

Diaphragm	
HR	% 86-Rb
40	1.17
PA 480	1.10
240	0.99
480	0.94
80	0.94
180	0.92
120	0.91
DH 12	0.91
360	0.85
740	0.78
600	0.73

Interscap. B.A.T.	
HR	% 86-Rb
360	5.83
600	5.19
120	5.06
240	4.76
480	4.31
180	4.08
40	3.33
740	2.62
80	2.34
DH 12	1.65
PA 480	1.52

Table 2 (continued)

Other B.A.T.		Total B.A.T.		Liver	
HR	% 86-Rb	HR	% 86-Rb	HR	% 86-Rb
360	4.82	360	10.64	PA 480	5.18
120	4.34	120	9.42	DH 12	5.00
240	4.24	600	9.39	120	3.31
600	4.20	240	9.00	740	3.30
180	3.86	180	7.93	600	3.27
480	3.33	480	7.65	40	3.16
740	2.22	40	5.53	80	2.45
40	2.20	740	4.84	240	1.60
80	1.99	80	4.33	480	1.50
DH 12	1.57	DH 12	3.22	360	1.41
PA 480	1.18	PA 480	2.70	180	1.34

Kidneys		Stomach		Intestine	
HR	% 86-Rb	HR	% 86-Rb	HR	% 86-Rb
PA 480	5.54	PA 480	1.30	PA 480	5.64
DH 12	2.74	740	1.30	DH 12	5.21
740	1.99	DH 12	1.20	40	4.36
600	1.55	80	1.11	740	3.02
40	1.54	40	1.00	80	2.19
480	1.12	240	0.77	600	1.69
80	1.09	600	0.69	480	1.48
180	0.88	480	0.67	240	1.19
120	0.85	120	0.66	120	1.13
360	0.75	180	0.46	360	1.13
240	0.65	360	0.46	180	0.76

Table 2 (continued)

Myocardium		Blood	
HR	% 86-Rb	HR	% 86-Rb
DH 12	5.85	120	14.71
120	5.28	40	13.79
480	5.03	240	12.54
360	5.02	360	11.61
240	4.89	80	11.51
600	4.71	DH 12	11.41
740	4.35	480	10.86
180	3.82	600	10.54
PA 480	3.82	180	10.26
40	3.46	740	10.15
80	3.36	PA 480	10.12

W.A.T.		Carcass	
HR	% 86-Rb	HR	% 86-Rb
PA 480	1.79	DH 12	26.05
360	1.36	40	21.73
80	1.17	80	20.31
DH 12	1.08	180	20.16
740	1.05	120	19.70
600	1.05	480	19.28
240	0.94	360	17.98
120	0.88	240	17.82
480	0.88	PA 480	17.15
180	0.85	600	17.08
40	0.75	740	14.61

Table 3. Results from statistical analysis on percentages (%) of injected 86-Rb (Rubidium) per organ or tissue of *E. fuscus*, sacrificed during deep hibernation (DH), at various heart rates (HR) during the arousal from hibernation, and during post-arousal (PA) in the summer (S) and in the winter (W).

Skin			Muscle ant. body			Muscle post. body		
HR		% 86-Rb	HR		% 86-Rb	HR		% 86-Rb
DH	12	S W	DH	12	W S	DH	12	W S
	40	S W		40	W S		40	S W
	80	S W		80	S W		80	S W
	120	S W		120	W S		120	W S
	180	S W		180	S W		180	S W
	240	S W		240	S W		240	S W
	360	S W		360	S W		360	S W
	480	S W		480	S W		480	S W
	600	S W		600	S W		600	W S
740-800		S W	740-800		S W	740-800		S W
PA	480	S W	PA	480	S W	PA	480	W S

S: refers to the mean percentage of injected 86-Rb per organ or tissue of bats, sacrificed during the summer.

W: refers to the mean percentage of injected 86-Rb per organ or tissue of bats, sacrificed during the winter.

Table 3 (continued)

Total muscle			Diaphragm			Interscap. B.A.T.		
HR		% 86-Rb	HR		% 86-Rb	HR		% 86-Rb
DH	12	W S	DH	12	S W	DH	12	W S
	40	W S		40	S W		40	W S
	80	S W		80	S W		80	W S
	120	W S		120	S W		120	W S
	180	S W		180	S W		180	W S
	240	S W		240	S W		240	W S
	360	S W		360	W S		360	W S
	480	S W		480	W S		480	W S
	600	S W		600	W S		600	W S
740-800		S W	740-800		W S	740-800		W S
PA	480	S W	PA	480	S W	PA	480	W S

Table 3 (continued)

Other B.A.T.		Total B.A.T.		Liver	
HR	% 86-Rb	HR	% 86-Rb	HR	% 86-Rb
DH 12	W S	DH 12	W S	DH 12	W S
40	W S	40	W S	40	S W
80	W S	80	W S	80	S W
120	W S	120	W S	120	S W
180	W S	180	W S	180	S W
240	W S	240	W S	240	S W
360	W S	360	W S	360	W S
480	W S	480	W S	480	W S
600	W S	600	W S	600	S W
740-800	W S	740-800	W S	740-800	S W
PA 480	W S	PA 480	W S	PA 480	W S

Table 3 (continued)

Kidneys			Stomach			Intestine		
HR		% 86-Rb	HR		% 86-Rb	HR		% 86-Rb
DH	12	S W	DH	12	S W	DH	12	S W
	40	S W		40	S W		40	S W
	80	S W		80	S W		80	S W
	120	S W		120	S W		120	S W
	180	S W		180	S W		180	S W
	240	S W		240	S W		240	S W
	360	S W		360	S W		360	S W
	480	S W		480	S W		480	S W
	600	S W		600	S W		600	S W
740-800		S W	740-800		S W	740-800		S W
PA	480	S W	PA	480	S W	PA	480	S W

Table 3 (continued)

Myocardium		Blood		W.A.T.	
HR	% 86-Rb	HR	% 86-Rb	HR	% 86-Rb
DH 12	S W	DH 12	W S	DH 12	W S
40	S W	40	W S	40	W S
80	S W	80	W S	80	W S
120	S W	120	S W	120	W S
180	W S	180	W S	180	W S
240	S W	240	S W	240	W S
360	S W	360	W S	360	S W
480	W S	480	W S	480	W S
600	S W	600	W S	600	W S
740-800	W S	740-800	W S	740-800	W S
PA 480	S W	PA 480	W S	PA 480	W S

Table 3 (continued)

		Carcass	
	HR		% 86-Rb
DH	12	W	
		S	
	40	W	
		S	
	80	W	
		S	
	120	W	
		S	
	180	W	
		S	
	240	W	
		S	
	360	S	
		W	
	480	W	
		S	
	600	W	
		S	
	740-800	W	
		S	
PA	480	W	
		S	

E. fuscus, sacrificed at different heart rates (HR) during the arousal

(T_a = 5 C) IN WINTER

240 8		300 8		360 8		480 8		600 8	
Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)	Mean	s_d (±)
2.52	0.32	2.59	0.46	2.80	0.61	2.59	0.42	4.12	0.50
34.78	2.25	33.14	3.56	36.48	3.20	37.10	2.77	38.89	1.98
4.04	0.46	4.97	1.19	4.26	1.11	2.94	0.62	4.39	0.60
38.81	2.31	38.11	3.87	40.72	2.93	40.04	3.00	43.28	2.21
0.82	0.15	0.86	0.32	0.95	0.23	0.97	0.24	0.84	0.16
13.74	2.54	11.01	3.20	9.39	2.18	9.60	1.99	7.16	0.86
10.40	2.50	9.47	2.78	7.67	1.50	7.95	1.77	5.74	0.69
24.13	4.55	20.47	5.79	17.07	3.36	17.59	3.58	12.91	1.34
1.27	0.40	1.58	0.47	1.60	0.40	1.80	0.61	1.92	0.69
0.48	0.23	0.51	0.13	0.42	0.14	0.70	0.10	0.41	0.09
0.28	0.04	0.31	0.12	0.34	0.11	0.38	0.12	0.38	0.16
0.51	0.10	0.50	0.17	0.62	0.20	0.83	0.25	0.58	0.19
4.13	0.40	4.90	0.91	4.85	0.81	5.78	0.68	4.82	0.43
12.40	2.80	13.21	2.20	13.31	1.98	13.68	1.83	12.57	1.60
1.50	0.51	1.84	0.78	1.34	0.74	1.13	0.49	1.76	0.49
13.14	1.52	15.11	2.30	15.97	1.35	14.51	2.53	16.40	0.91