Ornis Fennica 76:211–219. 1999

Energy metabolism and body temperature in the Blue-naped Mousebird (*Urocolius macrourus*) during torpor

Ralph Schaub, Roland Prinzinger and Elke Schleucher

Schaub, R., Prinzinger, R. & Schleucher, E., AK Stoffwechselphysiologie, Zoologisches Institut, Johann Wolfgang Goethe-Universität, Siesmayerstraße 70, 60323 Frankfurt/Main, Germany

Received 13 March 1998, accepted 15 September 1999

Mousebirds (Coliiformes) respond to cold exposure and food limitation with nightly bouts of torpor. During torpor, metabolic rate and body temperature decrease markedly, which results in energy savings. The decrease in body temperature is a regulated phenomenon as is also the arousal which occurs spontaneously without external stimuli. During arousal, Blue-naped Mousebirds warm at a rate of 1°C/min. This process requires significant amounts of energy. Our calculations show that the overall savings for the whole day are 30% at an ambient temperature of 15°C when daylength is 10 hours. Using glucose assays and RQ measurements, we found that during fasting, the birds switch to non-carbohydrate metabolism at an early phase of the day. This may be one of triggers eliciting torpor. By using cluster analysis of glucose levels we could clearly divide the night phase into a period of effective energy saving (high glucose levels) and arousal (low glucose levels).

1. Introduction

The aim of this study is to get information about the daily energy demand and the thermal regulation in small birds. For this we used the African Blue-naped Mousebird (*Urocolius macrourus*). Mousebirds are endemic to Africa. They belong to an order of their own, the Coliiformes (Schifter 1985), in which they form the one and only family, the *Coliidae*. In this class there are 6 species (Sibley & Alquist 1985).

The range of distribution reaches from the 5th to the 15th degree of latitude, where they prefer the arid and semi-arid thornbush and steppe areas, which on the one hand guarantees safety and on the other hand offers the basis for their special kind of food. Mousebirds are herbivorous. They feed mainly on leafs, buds and fruits (Schifter 1972). This kind of nutrition is low in energy, so the birds may face periods of energy deficiency (Schifter 1972). To survive these times of starvation, they have developed a special physiological strategy known as torpor. Torpor is a state in which metabolism and body temperature are decreased to a very low level, thus saving energy (Prinzinger 1982). Entrance into, maintenance of and arousal from torpor are active and regulated processes (Swan 1974). In birds, torpor is known in the species of the orders Caprimulgiformes, Apodiformes, Trochiliformes, and also in the Coliiformes.

We have studied earlier the metabolic rate and body temperature during the state of torpor in different mousebird species (Hoffmann & Prinzinger 1984). In the present study we add parallel measurements of blood glucose levels. With a correlation of these parameters it is possible to get in-

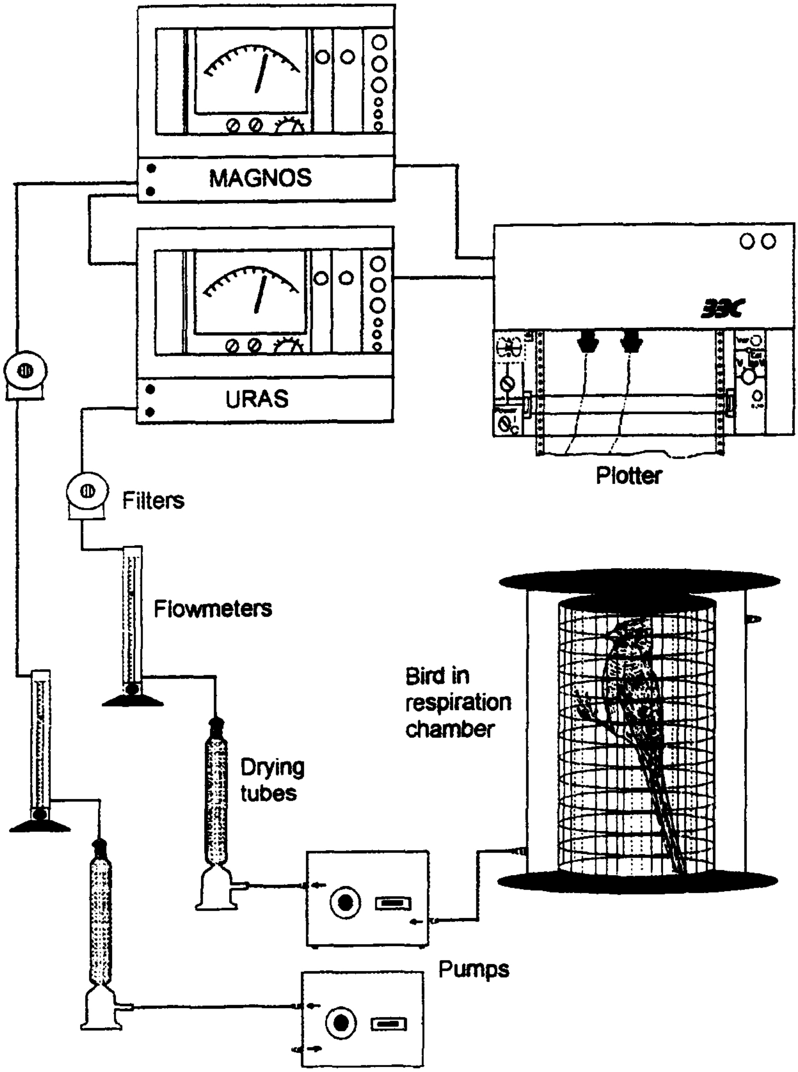

Fig. 1. The open flow system used for the measurements showing the bird in the incubation chamber, pumps, flowmeters, filters and the gas analyzers MAGNOS and URAS.

formation about theåsupply and demand of energy.

2. Material and methods

Energy consumption was measured by the method of the indirect calorimetry using the determination of O_2-consumption and CO_2-production. For this, the oxygen consumption was measured in an open flow system with a Hartmann & Braun MAGNOS 4G paramagnetic O_2-analyzer and the CO_2-production was measured in parallel with a Hartmann & Braun URAS CO_2-analyzer (Fig. 1). The bird was sitting in a cage, which stood in a cylindrical respiration chamber (40 x 25 cm). Effluent air was adjusted to 40l/h by calibrated flowmeters (Rota L 2.5) and special respirometer pumps (Wisa). Air was dried with $CaCl_2$ in specially designed drying tubes (Wertheim). All gas volumes were converted to their respective STPD values. MR was calculated in J/g*h (for conversion to W: 1 J/h = 0.278 mW) based on VO_2 (1 ml O_2 = 20 J) and the body mass measured on the same day (see below). A second channel served as a zero-point channel.

In parallel to these investigations, the body temperature was monitored, too. To get continu-

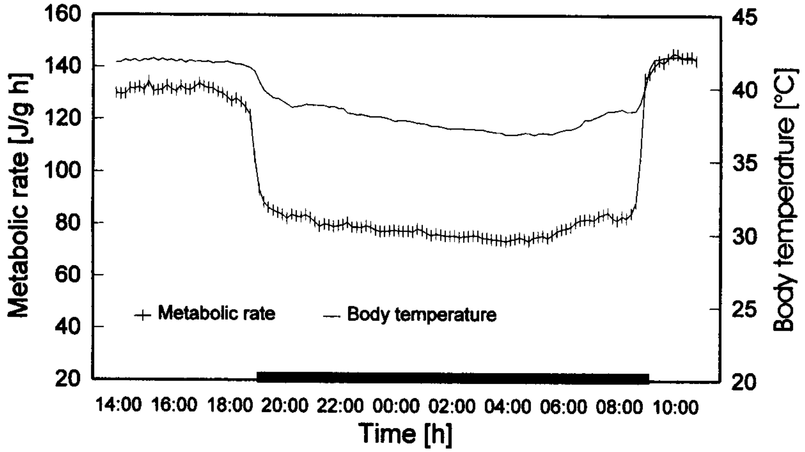

Fig. 2. Time course of metabolic rate (J/g*h) and body temperature (°C) with food *ad libitum* in Blue-naped Mousebirds (n = 26). The black bar represents the night phase.

ous data from undisturbed animals we used a telemetric method. For this, a transmitter was implanted into the peritoneal cavity of the bird. The transmitter signals were received from an antenna which was positioned above the cage. All data, oxygen consumption, CO_2-production and body temperature were shown on a plotter (Prinzinger et al. 1992).

Plasma glucose concentration was determined by an instrument designed for diabetics, which is normally used in human medicine (Diascan-S, Haselmayer).

17 adult individuals of the species *Urocolius macrourus* were used in this study. All birds were 3–5 years old, their mean body mass averaged from 53 to 55 g when fed *ad libitum* and down to 43 g during the experiments with reduced food. No data on sexual differences in energy metabolism could be observed. During the experiments the birds were held in climatic chambers at 15 ± 1°C. They were fed with bananas and apples, first given *ad libitum* and later on reduced rations to induce fasting torpor.

Each experiment lasted 6–7 days, interrupted only to clean the chamber and add new food. The birds were held in a light: dark regime of 10:14hr (day from 9 a.m. to 19 p.m., night from 19 p.m. to 9 a.m.). The long night phase is necessary for inducing torpor. At 1 p.m. the birds were brought into the metabolic chamber. One hour was allowed for the bird to adjust to the experimental conditions. At 11 a.m. on the following day the measuring series were finished and the setup was prepared for the next day. Because of this there is a data gap in the results.

3. Results

3.1. Metabolic rate and body temperature

In Fig. 2 a clearly diurnal cycle in both parameters can be seen. The average value during daytime for the metabolic rate is 134.6 ± 11.9 J/g*h, during the night it decreases to 79.7 ± 8.1 J/g*h, a decrease of about 41%. The course of the body temperature behaves in a similar matter. During the day an average value of 41.8 ± 0.7°C is observed. During the nighttime it decreases to 37.9 ± 1.4°C.

After these experiments food was reduced to induce torpor. To be sure that the birds were not put to a risk we reduced food successively over about three days. During this time a change in the investigated parameters could be monitored.

Fig. 3 shows the effect of three days of food reduction. On the first day there are nearly no changes in metabolic rate and body temperature. During daytime the metabolic rate is about 131 J/g*h, during the night it decreases to about 80 J/g*h. Body temperature varies between 41.5°C during the activity phase and 37.6°C in the resting phase. The second day shows more reduction, 128 J/g*h and 40.9°C during day and 65 J/g*h and 33.9°C during night. The third day, the last one before entering torpor shows a metabolic rate of about 128 J/g*h for the day, 48 J/g*h for the night and body temperature values of about 39.9°C for the day and 28.2°C for the night.

After these three days the birds were able to

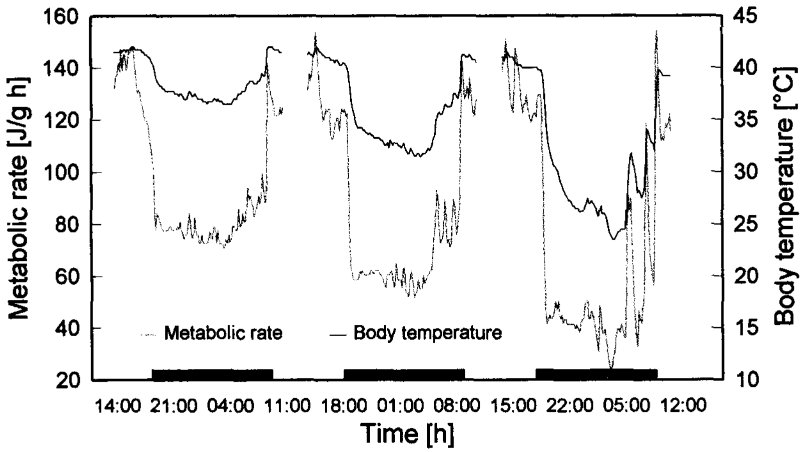

Fig. 3. Time course of metabolic rate (J/g*h) and body temperature (°C) during three successive days after food reduction in Blue-naped Mousebirds (n = 26). The black bars represent the night phases.

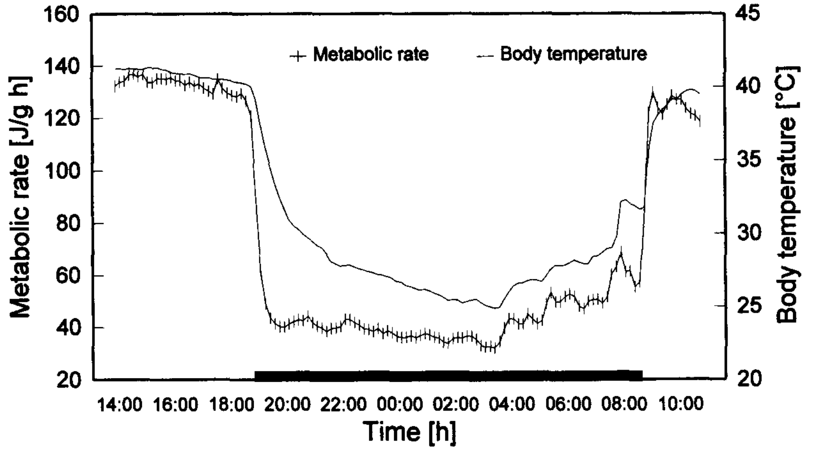

Fig. 4. Time course of metabolic rate and body temperature during torpor nights in Blue-naped Mousebirds (n = 11). The black bar represents the night phase.

undergo the state of torpor. The results of these investigations are shown in Fig. 4. During the day the metabolic rate is similar to that before torpor. The average value is 130.1 ± 12.6 J/g*h. With beginning of the night it decreases rapidly. The state of torpor is reached very fast. The average value is 44.1 ± 16.2 J/g*h, the deepest 10-min average value is at 3:20 a.m. with about 23 J/g.h. About five hours before the beginning of the light phase the metabolic rate starts to increase in steps. Similarly there is nearly no change in the course of the body temperature during the day. The average value is 40.2 ± 0.9°C. With beginning of the night, body temperature decreases rapidly. During the night the value is in average 28.2 ± 3.7°C, which means a decrease of about 11°C. The lowest value can be monitored at 3:40 a.m. with about 23.5°C. The lowest single value within these experiments was about 22°C. But it is known from another mousebird species that values as low as 18°C can be reached (Prinzinger et al. 1981). Below this temperature the birds undergo uncontrolled hypothermia. Body temperature starts to increase about 5 hours before beginning of the light phase.

With the present results of the metabolic rate it is possible to calculate the energy savings of torpor.

Average values of metabolic rate with food *ad libitum* :

Day	135 J/g*h	×	10 hours	=	1350 J/g
Night	80 J/g*h	×	14 hours	=	1120 J/g
			sum	=	2470 J/g

multiplicated with an average body mass of 50g:
total sum = 123 500 J/d

Calculation of metabolic rate with torpor: the

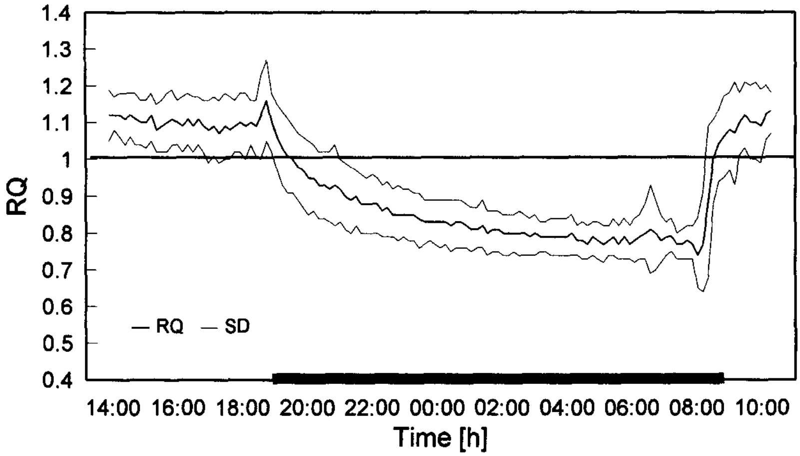

Fig. 5. Time course of the respiratory quotient with food *ad libitum* in Blue-naped Mousebirds (n = 26). The black bar represents the night phase, the thin lines the range of ± SD.

birds needed about 30 min to reach deep torpor and started their arousal phase about 350 min before the beginning of the day, so there exists a time gap of about 5 hours and 50 min with an intermediate metabolic behaviour.

Day 130 J/g*h × 10 hours = 1300 J/g
30 min of decreasing metabolic rate= 34 J/g
8 hours and 10 min of deep torpor = 310 J/g
Arousal phase = 272 J/g
sum = 1 916 J/g
multiplicated with an average body mass of 45g:
total sum =86 220 J/d

Hence, the energy saving for mousebirds in torpor is about 30.2%

3.2. The respiratory quotient

The CO_2-production was measured parallel with the O_2-consumption so the respiratory quotient could be calculated. RQ with food *ad libitum* is shown in Fig. 5. Before beginning of the night, RQ is 1.1 ±0.07. About 50 min after beginning of the night phase the value of 1 is reached. In the following hours it decreases successively. With a RQ over 1 the organism builds fat depots. The mean value during the night is 0.86 ± 0.06. It is not possible to make any statements which kinds of energy source were used in particular. 20 min after beginning of the light phase the RQ has increased to values above 1, which means the birds begin to change their metabolic sources of energy. With reduced food on a day with torpor the course of the RQ is different (Fig. 6). Almost 3 hours before night phase the RQ decreases below 1. Apparently the birds have to start using their internal reserves at a very early stage of the day.

3.3. Blood glucose level

Blood glucose levels show a clear diurnal cycle, too. During the activity phase, the mean value is 230.2 ± 20.1 mg/dl, in the night it decreases to 179.5 ± 13.8 mg/dl (Fig. 7). During the nights with torpor, the mean value of glucose concentration was 186.2 ± 64.8 mg/dl, even higher than the mean value during normothermic status. It is not possible to show day-values of the glucose concentration right before torpor nights. If blood was sampled in these critical times the birds did not undergo torpor in the following nights.

After the investigations of the metabolic rate and body temperature it was expected that the concentration of blood glucose would decrease in the state of torpor, too. To get an explanation for these data, the single "torpor-values" were subjected to a cluster analysis. This statistical investigation shows, that there are two different groups of values. Fig. 8 shows the individual values of blood glucose concentration during the phase of torpor. The circles represent the ascertained clusters. The first cluster extends from 4:10 a.m. to 6:40 a.m., the second from 7:10 a.m. to 8:40 a.m. For the first cluster the mean value is about 214 mg/dl, much higher than the mean value for

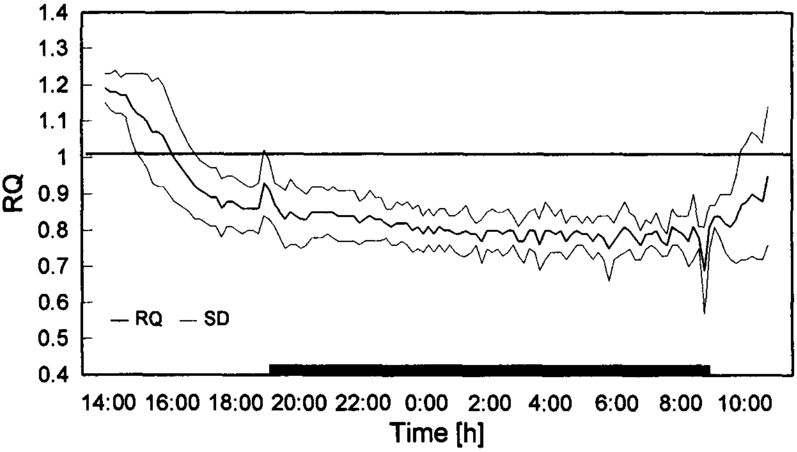

Fig. 6. Time course of the respiratory quotient during torpor nights in Blue-naped Mousebirds (n = 11). The black bar represents the night phase.

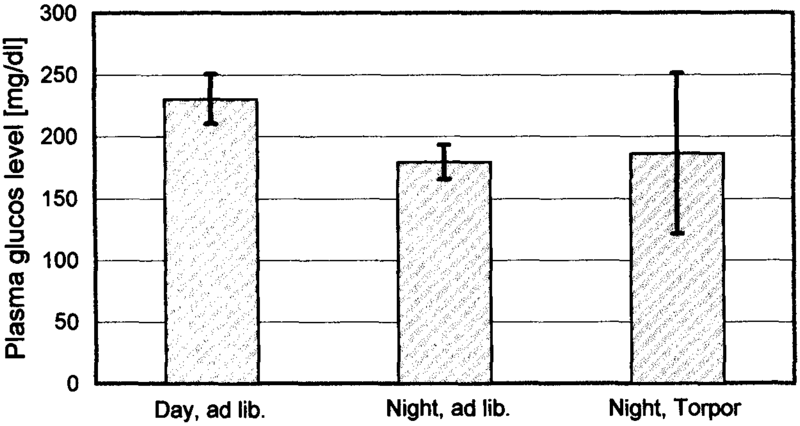

Fig. 7. Mean values of plasma glucose concentration (mg/dl) for day and night with food *ad libitum* and torpor nights.

the night with food *ad lib*. The second group has a mean value of about 136 mg/dl.

With these data it was possible to correlate these cluster values with the already known course of the metabolic rate during the torpor night. Fig.9 shows this part of the data from 4:00 a.m. to 10:50 a.m. during the state of torpor. The first cluster with the high mean value of 214 mg/dl fits temporally to the area of the deep torpor. The second cluster with the lower mean value of 136 mg/dl fits to the time of the arousal phase.

4. Discussion

It is common that birds show a diurnal decrease of the metabolic rate during the resting phase (Aschoff & Pohl 1970b). Most species show a decrease of about 50% but wide variations have been reported. Bezzel and Prinzinger (1990) measured decreases of about 75–80%, Aschoff and Pohl (1970a) show a mean decrease of about 24%. The mousebirds showed a clearly visible diurnal rhythm with mean values of 134.6 ± 11.9 J/g*h during the activity phase and 79.9 ± 8.1 J/g*h during the resting phase, which represents a decrease of about 41%. With this they range within the metabolic day-night differences of birds in general (Prinzinger 1988).

Different results have been reported on the body temperature of small birds during torpor. In most cases these large differences have methodological causes (Prinzinger et al. 1991). Reinertsen (1982) showed that cloacal and proventricular temperature recordings produced dissimilar results. The peripheral areas of the body can even behave in an "ectothermic" way. So, to get exact results it is necessary to measure the temperature of the inner body. The telemetric method seems to be the best way to get reliable values over a

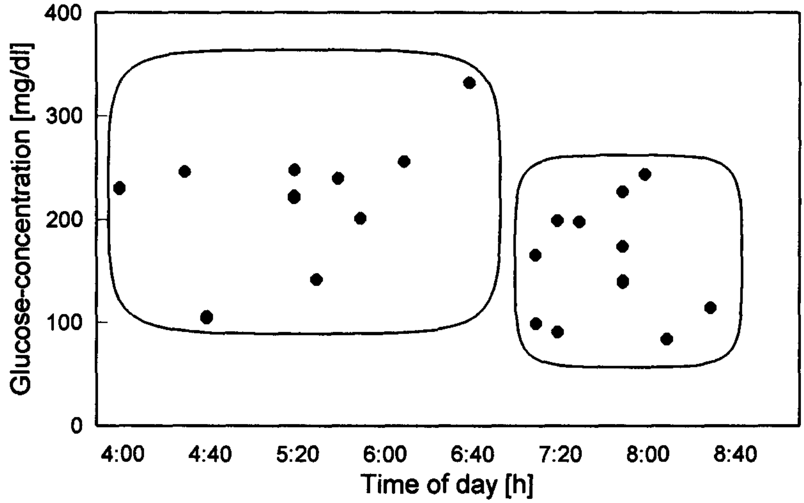

Fig. 8. Single values of blood glucose concentration with two clusters.

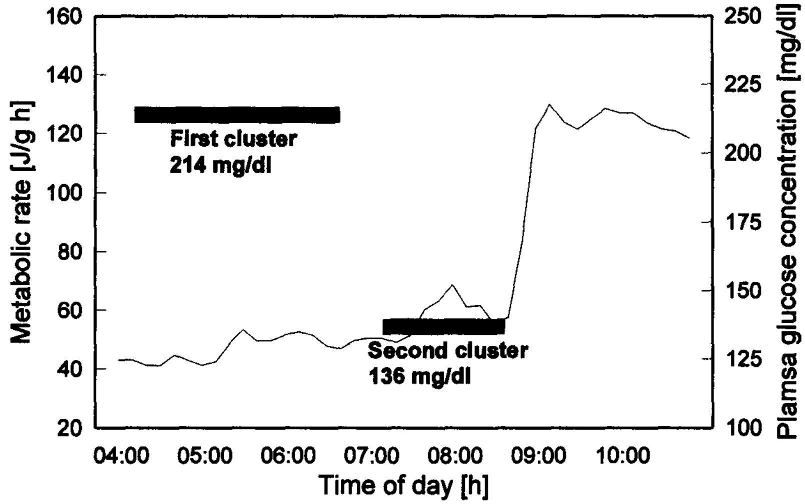

Fig. 9. Mean values of metabolic rate (line) in correlation with the mean values of the cluster analysis (bars).

long time and the measuring error is very small (Southwick 1973).

Body temperature showed a diurnal cycle, too. The investigated mousebirds had a mean body temperature of 41.8 ± 0.7°C during the day and of 37.9 ± 1.1 °C during the night. These results range within the temperatures which have been measured in other mousebird species with temperature values of about 40–42°C during day and 37–39°C during night (Bezzel & Prinzinger 1990, Prinzinger et al. 1991).

During torpor, the time courses of metabolic rate and body temperature changed. The metabolic rate began to decrease about 5 hours before end of day. This resulted from the fact that the birds had eaten their reduced food within one hour. In all investigations the birds reached torpor within 90 min after beginning of the night. They had to "hurry" to reach the energy saving state of torpor. As the total savings in torpor are about 30%, the birds cannot undergo torpor by the "wait and see" method. With beginning of the night they have to decide whether to undergo torpor or not. Under normal food conditions the metabolic rate was reduced about 41%, under torpor conditions it was reduced to about 66%. Another species of mousebirds has shown reductions of about 95% (Prinzinger et al. 1981).

Body temperature varied in a similar way. The mean value during torpor was 28.2 ± 3.8°C, the lowest single value was about 22°C. Investigations with Redbacked Mousebirds have shown that the lowest body temperature for birds with a body mass of about 45 g is about 18°C. It is not possible for the birds to recover from lower body temperatures. When the day started, the birds never had a body temperature over 40°C, which shows that they had no chance to reach their standard activity body temperature because of energy deficiency.

Considering that there was no change in ambient temperature or illumination this must be an endogenous, regulated phenomenon. The body temperature of endothermic organisms is maintained by the heat which originates from metabolic work. When metabolic rate and body temperature are correlated it seems that both parameters evolve in the same time schedule. But one of them must be the regulated one and influence the other. During torpor or hibernation the metabolic rate is decreased to a low level. This reduction can be explained with temperature dependent biochemical mechanisms which follow the Q_{10}-rule. In this case the body temperature would be the active regulated parameter (Koolman & Röhm, 1994). But if the deepest metabolic rates and the deepest body temperatures in the presented data are taken as fixed points, it can be seen that the metabolic rate changes earlier than the body temperature.

Similar results were found in Siberian hamsters (Heldmaier & Ruf 1992). There was a difference of about 2 hours between the lowest values of these parameters. For another species of hamsters a time gap of about 5 hours could be seen (Lyman 1948) and for hibernating marmots up to 12 hours (Lyman 1958). For hibernating squirrels it was even more than 12 hours (Wang 1978, 1989). The length of these time gaps results from the variable body masses of the animals. Torpor can mostly be seen in animals in which body mass is below 100g (Heldmaier 1993). With a small body mass and a large relative surface area the changes in metabolic rate and body temperature are very fast.

The blood glucose level showed a diurnal cycle, too. In the present study the concentration decreased by about 22%. Other species of birds have shown similar diurnal cycles of the plasma glucose. The changes must be endogenous because they seem to be independent from body mass, activity or food (Dolnik 1973). Umminger (1977) has suggested that all vertebrates show changes of glucose concentration during activity and resting phase.

The interesting fact is that glucose concentration is about 3.6% higher during torpor than in nights with food *ad libitum*. Cluster analysis showed that during deep torpor the level of plasma glucose is about 16% higher than with food *ad libitum* but that in the time of arousal it is about 32% lower. At this time the birds need more energy to wake up from torpor. The question is what is the torpor inducing factor. Previous studies show that animals have to lose body mass (Schifter 1972). But this cannot be the only point. It is known from investigations with Siberian hamsters (Dark & Zucker 1984) that the availability for glucose is the torpor inducing factor. The hamsters that got an injection of 2-desoxy-glucose, a glucose analogue which inhibits glycolysis, underwent torpor in the following night although they had food *ad libitum* and did not show loss of body mass. In the present study the glucose level was extremely high during torpor. This suggests that a biochemical switch stops glucose consumption. Evidence for this hypothesis is provided by the fact that on the day before torpor the RQ decreases very rapidly below 1 which means that non-carbohydrate energy resources were used to maintain metabolic rate. More elaborate methods for glucose sampling are needed to elucidate this question.

Selostus: **Sininiskahiirilinnun (*Urocolius macrourus*) aineenvaihdunta ja ruumiinlämpötila yöllisen horroksen aikana**

Hiirilinnut pystyvät nälkä- ja kylmästressissä vaipumaan lyhytkestoiseen yölliseen horrokseen, jonka aikana ne ovat täysin liikkumattomia. Tämän vaiheen aikana laskevat aineenvaihdunta ja ruumiinlämpötila minimiin, jolloin energiaa säästyy. Vaikka aineenvaihdunta alenee jopa 50% ja ruumiinlämpötila laskee jopa 22°C:een, kyseessä on aktiivinen, sisäisesti säädelty tapahtuma. Samoin herääminen ja siihen liittyvä lämpötilan nousu aamulla on spontaani. Heräämisvaiheessa ruumiinlämpötila nousee enimmillään 1°C/min.

Mittaamalla veren glukoosipitoisuuksia ja RQ-arvoa (aineenvaihdunnan tuottaman hiilidioksidin määrän suhde kulutettuun hapen määrään), havaitsimme että ravinnon puute aikaansaa siirtymisen elimistön rasvavarojen käyttöön energialähteenä, mikä mahdollisesti toimii horrostilan eräänä laukaisutekijänä. Syvimmän horrosvaiheen aikana veren sokeritaso oli paastoavilla linnuilla korkeammalla kuin kontrollilinnuilla samassa vaiheessa, mikä tukee oletusta, että horrostilan tärkein funktio on säästää kudosten energiavarastoja. Vaikka horrostilan aikana aineenvaihdunta laskee jopa yli 50%, horrostilan tuoma kokonaissäästö oli 30%, koska päiväajaksi aineenvaihdunta palautuu lähes normaaliksi.

Acknowledgements. This study was supported by a grant of the Deutsche Forschungsgemeinschaft DFG (Pr 205/5-1).

References

Aschoff, J. & Pohl, H. 1970a: Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. — J. Orn. 111: 38–47.

Aschoff, J. & Pohl, H. 1970b: Rhythmic variations in energy metabolism. — Fed. Proc. 29: 1541–1552.

Bezzel, E. & Prinzinger, R. (1990): Ornithologie. — UTB für Wissenschaft, Große Reihe, Verlag E. Ulmer, Stuttgart.

Dark, C. G. & Zucker, L. M. 1994: Reduced glucose availability induces torpor in siberian hamsters (Phodopus sungorus). — Am. J. Physiol. 267: R496–R501.

Dolnik, T. V. 1973: Diurnal and seasonal cycles of the blood sugar in sedentary and migrating birds. — Zoll. Zu. 52: 94–103.

Heldmaier, G. & Ruf, T. 1992: Body temperature and metabolic rate during natural hypothermia in endotherms. — J. Comp. Physiol. B 162: 696–706.

Heldmaier, G. 1993: Seasonal acclimatization of small mammals. — Verh. Dtsch. Zool. Ges. 86(2): 67–77.

Hoffmann, R. & Prinzinger, R. 1984: Torpor und Nahrungsausnutzung bei 4 Mausvogelarten (Coliiformes). — J. Orn. 125: 225–237.

Koolman, J. & Röhm, K. H. 1994: Taschenatlas der Biochemie. — Stuttgart; New York. Thieme-Verlag.

Lyman, C. P. 1948: The oxygen consumption and temperature regulation of hibernating hamsters. — J. Exp. Zool. 109: 55–78.

Lyman, C. P. 1958: Oxygen consumption, body temperature and heart rate of woodchucks entering hibernation. — Am. J. Physiol. 194: 864–869.

Prinzinger, R. 1982: Mausvögel (Coliiformes). Geheimnisvolle Vegetarier aus Afrika. — Die Voliere 5, Heft 3: 88–90.

Prinzinger, R. 1988: Energy metabolism, body-temperature and breathing parameters in nontorpid blue-naped mousebirds *Urocolius macrourus*. — J. Comp. Physiol. B 157: 801–806.

Prinzinger, R., Göppel, R. & Lorenz, A. 1981: Der Torpor beim Rotrückenmausvogel Colius castanotus. — J. Orn. 122: 379–392.

Prinzinger, R., Preßmar, A. & Schleucher, E. 1991: Body temperature in birds. — Comp. Biochem. Physiol. 99A: 499–506.

Prinzinger, R., Schleucher, E. & Preßmar, A. 1992: Langzeittelemetrie der Körpertemperatur mit synchroner Bestimmung des Energiestoffwechsels beim Blaunackenmausvogel (Urocolius macrourus) unter Normal- und Lethargiebedingungen (Torpor). — J. Orn. 133: 446–450.

Reinertsen, R. E. 1982: Radio telemetry measurements of deep body temperatures of small birds. — Ornis Scand. 13: 11–16.

Schifter, H. 1972: Die Mausvögel. — Die neue Brehm-Bücherei 459, A. Ziemsen-Verlag, Wittenberg-Lutherstadt.

Schifter, H. 1985: Systematics and distribution of Mousebirds (Coliidae). — Proc. Intern. Symp. African Vertebr., Bonn, Museum A. Koenig: 325–347.

Sibley, C. G. & Alquist, J. E. 1985: The relationship of some groups of african birds, based on comparisons of the genetic material, DNA. — Proc. Intern. Symp. African Vertebr., Bonn, Museum A. Koenig: 115–151.

Southwick, E. E. 1973: Remote sensing of body temperature in a captive 25g bird. — Condor 75: 464–466.

Swan, H. (1974): Thermoregulation and bioenergetics. — Amer. Elsevier Publ. Comp., New York, London, Amsterdam.

Umminger, B. L. 1977: Relation of whole sugar concentrations in vertebrates to standard metabolic rate. — Comp. Biochem. Physiol. 56A: 457–460.

Wang, L. C. H. 1978: Energetics and field aspects of mammalian torpor: the Richardson's ground squirrel. — In: Wang, L. C. H. & Hudson, J. W. (eds), Strategies in cold, natural torpidity and thermogenesis. Academic Press, New York: 109–145.

Wang, L. C. H. 1989: Ecological, phsyological, and biochemical aspects of torpor in mammals and birds. — Advance in Comp. and Env. Phys. Vol. 4. Springer-Verlag, Berlin, Heidelberg.