The Condor 99:113–122

DIURNAL VARIATION OF METABOLIC RESPONSES TO SHORT-TERM FASTING IN PASSERINE BIRDS DURING THE POSTBREEDING, MOLTING AND MIGRATORY PERIOD[1]

SUSANNE JENNI-EIERMANN AND LUKAS JENNI
Swiss Ornithological Institute, CH-6204 Sempach, Switzerland,
e-mail: jennil@orninst.ch

Abstract. Prior studies have shown that plasma metabolite levels differ between feeding and short-term fasted passerines. This study investigates whether the metabolic response to short-term fasting varies during the course of the daylight hours or between birds during the postbreeding, molting and migratory period. In four species of migratory passerines, six plasma metabolite levels were measured in short-term fasted and feeding birds. Compared with feeding birds, short-term fasted birds showed decreased plasma triglyceride and glucose levels, increased β-hydroxy-butyrate and free fatty acid levels, and stable uric acid levels. This indicates that short-term fasting birds use lipids from adipose tissues and from the diet, but do not spare protein and carbohydrates. Birds during the postbreeding, molting and migratory period generally showed a similar response to short-term fasting. The metabolic response to short-term fasting was modified during the course of the day. In the early morning, short-term fasted birds exhibited similar metabolite levels as overnight fasted birds. During the course of the day, β-hydroxy-butyrate levels increased progressively less during short-term fasting, probably as a consequence of restored glycogen stores and increased food-intake and lipid stores.

Key words: fasting, diurnal course, molt, migration, triglycerides, uric acid, free fatty acids, β-hydroxy-butyrate.

INTRODUCTION

Passerine birds generally feed during the day to cover energetic requirements during the day and for overnight fasting. Environmental factors may prevent or reduce food-intake during part or all of the day. The search for good feeding places and the defense of a territory, nest site or mate may be other factors reducing food intake during the day. For many ecological field studies, it is of great interest to discern birds with a reduced food-intake.

Earlier studies have shown that plasma metabolites are likely candidates for characterizing the feeding states of free-living birds caught only once in field studies. Plasma metabolite concentrations adequately characterize birds fasted for one or a few hours during the day in comparison with feeding and overnight fasted birds (Swain 1987, 1992, Jenni-Eiermann and Jenni 1991, 1996, Jenni and Jenni-Eiermann 1992). Experiments with caged Garden Warblers *Sylvia borin* revealed that change in body mass (as a measure of food intake) is correlated with several plasma metabolite concentrations (Jenni-Eiermann and Jenni 1994).

However, these studies did not address diurnal variations in plasma metabolite levels as they occur in feeding birds, nor the pattern of diurnal plasma metabolites during the postbreeding, molting and migratory period (Jenni and Jenni-Eiermann 1996).

Hence, the aim of this study was to investigate (a) whether the metabolic response to short-term fasting differs during the course of the daylight hours, i.e., whether it depends on the nutritional state before short-term fasting, and (b) whether the metabolic response to short-term fasting in migrant species differs between the postbreeding, molting and migration periods. This will allow more accurate recognition of temporarily fasted birds and birds with a deficit in food intake in the field.

MATERIALS AND METHODS

ANIMALS

During August, September and October 1986–1989, free-living European Robins (*Erithacus rubecula*), Blackcaps (*Sylvia atricapilla*), Garden Warblers (*S. borin*) and Pied-Flycatchers

[1] Received 15 May 1996. Accepted 30 October 1996.

(*Ficedula hypoleuca*) were caught throughout the daylight hours in mist nets on a bird-banding station at Lake Neuchâtel, Switzerland. Most birds caught were in their first year of life. The few adults did not differ from first-year birds in the plasma levels of the metabolites examined.

In all birds, the intensity of body feather molt (5 classes: 0 = no growing body feather, 4 = over 50% of body feathers growing) and the progress of molt (before, during, after molt) were determined and used to assign birds to one of three periods of the annual cycle: (1) the postbreeding period, which comprised birds before molt (juvenile plumage in first-year birds) or growing their first few feathers (molt intensity 0 or 1), (2) the molting period, which contained birds during molt (molt intensity 2–4), and (3) the migratory period, in which birds had completed molt or still had a few last feathers growing (molt intensity 0 or 1).

BLOOD SAMPLING, METABOLITES AND METABOLITE DETERMINATIONS

Some birds (n = 188) were kept singly in cotton bags and without food for 90–120 min to simulate temporary fasting during the day. They were compared with birds blood-sampled as quickly as possible after they flew into the mist net (Jenni-Eiermann and Jenni 1996). The diurnal variation in metabolite levels of these normally feeding birds is presented in detail elsewhere (Jenni and Jenni-Eiermann 1996).

Six plasma metabolites were investigated. Free fatty acids and glycerol usually indicate lipid mobilization from adipose tissues, because stored lipids (mainly triglycerides) need to be hydrolyzed to free fatty acids and glycerol before entering the blood. Plasma free fatty acid concentrations are regarded as being proportional to fatty acid release and oxidation, and plasma glycerol levels to glycerol turnover (Scow and Chernick 1970, Hurley et al. 1986, Elia et al. 1987). Therefore, in fasting birds, plasma free fatty acid and glycerol levels are expected to be higher than in feeding birds.

Most plasma triglycerides originate directly or via synthesis in the liver from the diet and indicate lipid transport to the peripheral tissues (Robinson 1970). Experiments with caged Garden Warblers fed different amounts of food indicated that plasma triglyceride levels are correlated with change in body mass and, thus, are indicators of migratory fattening (Jenni-Eiermann and Jenni 1994). In fasting birds, triglyceride levels are expected to be decreased.

β-hydroxy-butyrate is synthesized predominantly during fasting and replaces part of the glucose, especially in the brain (Robinson and Williamson 1980). Its plasma concentration is negatively correlated with change in body mass (Jenni-Eiermann and Jenni 1994) and, hence, an indicator of lipid catabolism, glucose shortage and fasting.

Uric acid is the end product of protein catabolism and its plasma concentration is an indication of protein breakdown (Mori and George 1978, Robin et al. 1987, Lindgård et al. 1992).

Plasma glucose levels are generally kept within narrow limits, but have been reported in some bird studies to vary in response to fasting (Swain 1987).

Blood sampling and analyses of plasma metabolite levels followed procedures described earlier (Jenni-Eiermann and Jenni 1991). Because the amount of blood collected varied, not all metabolites could be determined in all individuals. The triglyceride values given here include free glycerol. Since glycerol values were low compared with triglyceride values, we decided not to subtract free glycerol for the sake of a much more complete triglyceride data set.

DATA ANALYSIS

The frequency distributions of the triglyceride values deviated significantly from a normal distribution, but not if log-transformed. Hence the latter were used for all analyses. The frequency distributions of all other metabolite levels did not deviate, or only slightly deviated, from a normal distribution.

For each of the four species, the diurnal changes of each metabolite level of short-term fasted birds were compared with those of feeding birds (data from Jenni and Jenni-Eiermann 1996) for a maximum of three periods of the annual cycle. In order to allow for different slopes and intercepts of the relationship between time of day and metabolite, we used a multiple regression model in which physiological situation and period of the annual cycle were differentiated by dummy variables. The full model included the metabolite level as the dependent variable and the following independent terms:

T = time after dawn (hr).

S = physiological situation (dummy variable set at 0 for feeding birds and at 1 for short-term fasted birds) which gives the difference between the intercept of short-term fasted birds and the intercept of feeding birds.

S·T = difference in slope of the short-term fasted birds compared with that of feeding birds.

MP = difference in intercept for molting birds compared with that of birds in the postbreeding and migratory period (dummy variable set at 1 for molting birds and at 0 for birds in the postbreeding and migratory period).

PP = difference in intercept for birds in the postbreeding period compared with that of birds in the molting and migratory period (dummy variable set at 1 for birds in the postbreeding period and at 0 for birds in the molting and migratory period).

MP·T and PP·T = difference in slope for birds in the molting and postbreeding period, respectively, compared with that of the respective remaining birds.

MP·S and PP·S = difference in intercept of short-term fasted birds in the molting and postbreeding period, respectively, compared with that of the respective remaining short-term fasted birds.

MP·S·T and PP·S·T = difference in slope for short-term fasted birds in the molting and postbreeding periods, respectively, compared with that of the respective remaining short-term fasted birds.

For species without data for birds in the postbreeding period (Garden Warbler and European Robin) or with data for birds in the migratory period only (Pied Flycatcher), the full model was simplified accordingly.

Backward elimination procedures were used to identify the significant terms of the model. Significant terms S·T, MP·S·T or PP·S·T would indicate that the diurnal variation of short-term fasted birds is different from that of feeding birds. If these terms are not significant, significant terms S, MP·S or PP·S would indicate that short-term fasted birds have a lower or higher plasma concentration than feeding birds, but that both vary in parallel during the course of the daylight hours.

RESULTS

TRIGLYCERIDES

Since plasma triglyceride levels of feeding birds increased more steeply in the early morning than thereafter (Jenni and Jenni-Eiermann 1996), only data after the steep increase (i.e., after 1.6 hr, 3.0 hr and 3.6 hr after dawn in European Robin, Blackcap and Garden Warbler, respectively) were used for this analysis.

In short-term fasted birds of all four species, plasma triglyceride levels increased during the day at a similar rate as in feeding birds, but at a significantly lower level (Tables 1–4, example given in Fig. 1). In Blackcaps, short-term fasted birds reduced triglyceride levels to a similar extent in the molting and migratory period (MP·S not significant), whereas short-term fasted Blackcaps during the postbreeding period reduced triglyceride levels to a lesser extent than molting and migratory birds (PP·S positive and significant, Table 1).

Hence, short-term fasting resulted in a similar decrease of triglyceride levels at all times of the day and in the molting and migratory period, compared with feeding conspecifics after the steep early morning increase. Blackcaps exhibited a smaller, but again diurnally constant, decrease in the postbreeding period than during the molting and migratory period.

FREE FATTY ACIDS

Generally, plasma free fatty acid levels of short-term fasted birds did not show a diurnal trend (Tables 1–4, example given in Fig. 2a). Exceptions were Blackcaps (Fig. 2b) and Garden Warblers in the molting period which displayed a significant decrease of free fatty acid levels during the day (Table 1 and 3). A corresponding decrease, but at a lower level, also was found in feeding Blackcaps in the molting period, but not in feeding Garden Warblers (Jenni and Jenni-Eiermann 1996).

Hence, short-term fasted birds generally exhibited higher free fatty acid levels than feeding birds; exceptions were migratory Garden Warblers (European Robin not studied) and molting Garden Warblers in the afternoon.

TABLE 1. Multiple regression models of plasma metabolite concentrations of Blackcaps upon time after dawn, which allows for six different regression lines (feeding and short-term fasted birds in the postbreeding, molting and migratory period). The final result of a stepwise procedure is shown with only the terms significant at the $P < 0.05$ level. For glycerol, no significant terms remained. For the full model and the abbreviations of the variables see Methods.

Dependent variable	n	R^2_{adj}	F	Regression coefficients of independent variables: Constant	S	T	S · T	MP	PP	MP · T	MP · S	PP · S
ln(triglycerides)	108	0.48	21.1***	1.01***	−0.60***	0.04***	—	−0.25**	−0.47***	—	—	0.30*
Free fatty acids	134	0.25	15.5***	1.26***	0.36***	—	—	—	−0.50***	−0.04***	—	—
β-hydroxy-butyrate	128	0.62	103.2***	0.64***	3.33***	—	−0.12***	—	—	—	—	—
Glucose	146	0.33	36.0***	18.31***	−4.83***	0.29***	—	—	—	—	—	—
Uric acid	162	0.14	14.2***	0.61***	—	—	—	—	0.28***	—	0.27***	—

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

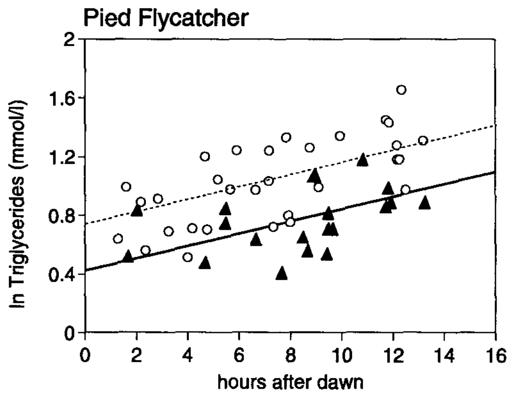

FIGURE 1. Regression of plasma triglyceride concentrations upon time after dawn in short-term fasted (triangles) and feeding (circles) Pied Flycatchers during the migratory period. Regression lines according to the multiple regression model (Table 4) are indicated for short-term fasted (solid line) and feeding birds (dotted line).

GLYCEROL

Plasma glycerol levels did not differ between short-term fasted and feeding birds and there was no diurnal trend. The only exception was a decrease during the day in short-term fasted Garden Warblers in the molting and migratory period (Table 3).

β-HYDROXY-BUTYRATE

In all species, plasma β-hydroxy-butyrate concentrations were much higher in short-term fasted birds than in feeding birds (Tables 1–4, examples given in Fig. 3), which was most marked in the European Robin. In the Blackcap, there was no difference in β-hydroxy-butyrate levels between the three periods of the annual cycle. However, short-term fasted Garden Warblers in the molting period showed higher levels than in the migratory period. During the day, short-term fasted birds exhibited a continuous decrease in β-hydroxy-butyrate levels (example given in Fig. 3b), with the exception of the Pied Flycatcher (Fig. 3a). Hence, the rise in β-hydroxy-butyrate due to short-term fasting was significantly larger in the morning than afterwards in three of the four species examined. European Robins and Garden Warblers at dawn, at the onset of feeding, also had high β-hydroxy-butyrate levels which dropped very quickly to low levels and showed no diurnal trend in feeding birds (Jenni and Jenni-Eiermann 1996).

TABLE 2. Multiple regression models of plasma metabolite concentrations of European Robins upon time after dawn, which allows for four different regression lines in the case of triglycerides and glucose (feeding and short-term fasted birds in the molting and migratory period) and for two regression lines in the case of free fatty acids, glycerol, β-hydroxy-butyrate, and uric acid (feeding and short-term fasted birds in the molting period). For explanations, see Table 1. For glycerol, no significant terms remained.

Dependent variable	n	R^2_{adj}	F	Regression coefficients of independent variables: Constant	S	T	S · T	MP
ln(triglycerides)	78	0.56	33.0***	1.03***	−0.49***	0.04*	—	−0.63***
Free fatty acids	41	0.21	11.6**	0.87***	0.36**	—	—	—
β-hydroxy-butyrate	21	0.90	87.5***	0.69*	4.47***	—	−0.11*	—
Glucose	104	0.11	5.4**	18.22***	−2.94**	0.31**	—	1.60*
Uric acid	44	0.22	13.0***	1.11***	−0.31***	—	—	—

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

GLUCOSE

In feeding birds, plasma glucose levels generally increased during the day, with the exception of the Garden Warbler. In short-term fasted birds, a similar increase during the day was found for all species, but at a lower level than in feeding birds (Tables 1–4, example given in Fig. 4). Hence, the drop in glucose level due to short-term fasting was similar over the daylight hours, with the possible exception of the Garden Warbler.

URIC ACID

In short-term fasted and feeding birds, plasma uric acid levels did not exhibit a diurnal trend, with the exception of short-term fasted Garden Warblers in the molting period (Tables 1–4). A significantly lower uric acid level in short-term fasted than in feeding birds was found in molting European Robins and a significantly higher level was found in molting Blackcaps.

DISCUSSION

Plasma glycerol, free fatty acid and uric acid concentrations were shown to be related to turnover (see literature cited in Jenni-Eiermann and Jenni 1996). Furthermore, experiments on caged Garden Warblers fed different amounts of food revealed that uric acid, triglyceride, glycerol, free fatty acid, and β-hydroxy-butyrate concentrations are correlated with the change in body mass during the day which is a measure of food intake (Jenni-Eiermann and Jenni 1994). Hence, the following discussion is based on the assumption that these plasma metabolite concentrations reflect turnover.

As presented in Jenni-Eiermann and Jenni (1991), the change in metabolite levels from

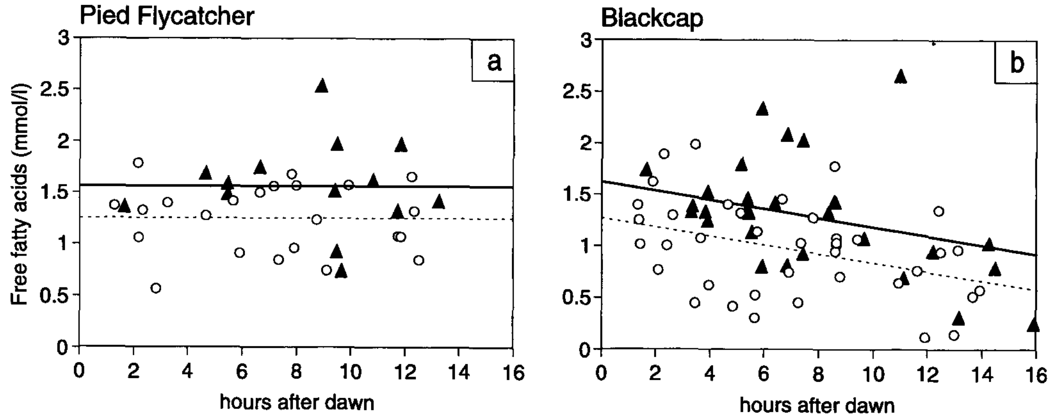

FIGURE 2. Regression of plasma free fatty acid concentrations upon time after dawn in (a) Pied Flycatchers during the migratory period and (b) Blackcaps during the molting period. See Figure 1 for explanations and Tables 1 and 4 for regression model.

TABLE 3. Multiple regression models of plasma metabolite concentrations of Garden Warblers upon time after dawn which allows for four different regression lines (feeding and short-term fasted birds in the molting and migratory period). See Table 1 for explanations.

Dependent variable	n	R^2_{adj}	F	Regression coefficients of independent variables						
				Constant	S	T	S · T	MP · T	MP · S	MP · S · T
ln(triglycerides)	63	0.23	7.4***	0.83***	−0.40***	0.05**	—	−0.03*	—	—
Free fatty acids	70	0.15	7.0**	0.98***	—	—	—	—	1.01***	−0.09**
Glycerol	73	0.10	8.7**	0.59***	—	—	−0.01**	—	—	—
β-hydroxy-butyrate	70	0.65	43.0***	0.73***	2.13***	—	−0.08**	—	0.87***	—
Glucose	100	0.11	7.2**	20.36***	−4.94***	—	0.46**	—	—	—
Uric acid	100	0.04	4.8*	0.74***	—	—	—	—	—	0.02*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

feeding to short-term fasting in individual European Robins and Garden Warblers blood-sampled twice (feeding and short-term fasted) was similar to the difference in mean values of feeding and short-term fasted birds blood-sampled once. Hence, we believe that the cross-sectional data on metabolite levels between individuals are valid indicators of changes within individuals.

METABOLIC RESPONSE TO SHORT-TERM FASTING

Short-term fasting entailed a decrease in plasma triglyceride and glucose levels and an increase in β-hydroxy-butyrate and free fatty acid levels, as shown in earlier studies (Jenni-Eiermann and Jenni 1991, 1996, Jenni and Jenni-Eiermann 1992).

Most plasma triglycerides originate directly or via synthesis in the liver from the diet and are transported to the peripheral tissues, especially the adipose tissues (Robinson 1970, Havel 1987). Plasma levels of triglycerides are correlated with the gain in body mass during the previous hours, which is a measure of fat deposition (Jenni-Eiermann and Jenni 1994). Hence, an interruption in food-intake soon results in a decrease in plasma triglyceride levels and probably a decrease in fat deposition. The interruption in food-intake provokes a transient decrease in glucose level, which helps to increase the hydrolysis of lipids from the adipose tissues into free fatty acids and glycerol (Klein et al. 1990). Indeed, in short-term fasted birds plasma free fatty acid levels were increased, which indicates the utilization of fatty acids from adipose tissues. β-hydroxy-butyrate, which is synthesized from free fatty acids, is well known to increase sharply as a reaction to fasting (Robinson and Williamson 1980, Jenni-Eiermann and Jenni 1991). It replaces glucose in those organs not able to catabolize fatty acids, especially in the brain. Plasma uric acid levels indicate net protein breakdown (Robin et al. 1987). They generally did not change in short-term fasted birds. This indicates that the sparing of protein which is typical for longer fasting periods (Cherel et al. 1988, Cherel and Le Maho 1988) did not yet start in our short-term fasted birds.

In the Horned Lark (*Eremophila alpestris*), 5 hr of fasting during the night also entailed an increase in plasma β-hydroxy-butyrate and free

TABLE 4. Multiple regression models of plasma metabolite concentrations of Pied Flycatchers upon time after dawn which allows for two different regression lines (feeding and short-term fasted birds in the migratory period). See Table 1 for explanations. For glycerol and uric acid, no significant terms remained.

Dependent variable	n	R^2_{adj}	F	Regression coefficients of independent variables		
				Constant	S	T
ln(triglycerides)	52	0.43	20.5***	0.74***	−0.32***	0.04***
Free fatty acids	37	0.13	6.3*	1.25***	0.32*	—
β-hydroxy-butyrate	41	0.69	91.7***	0.88***	3.16***	—
Glucose	45	0.66	44.1***	20.41***	−4.89***	0.23**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

fatty acids, but plasma glucose and triglyceride levels were similar to those in feeding birds sampled in the evening (Swain 1992). In that study, glucose levels may have been similar to feeding values because they had already returned to normal levels after a transient decrease as observed in our birds (Jenni-Eiermann and Jenni 1991) or because plasma triglycerides were not yet depleted. However, it is unclear to us, why plasma triglyceride levels of Horned Larks were still high after 5 hr of fasting. Such elevated triglycerides may be related to the fact that fasting in the Horned Lark study started in the evening when triglyceride levels are highest, whereas our study examined birds sampled predominantly during the morning and which had not yet accumulated large amounts of lipids.

In summary, short-term fasted birds during the day show a metabolic reaction different from overnight fasted birds. They apparently rely on lipids synthesized from the diet and hydrolyzed from adipose tissues as well as on carbohydrates and protein. They showed no indication of protein sparing. Hence, short-term fasting in small passerines is metabolically similar to the transitional first phase in long-term fasting large birds (Cherel et al. 1988).

DEPENDENCE ON THE PERIOD OF THE ANNUAL CYCLE

Triglyceride levels of feeding birds differ between the three periods of the annual cycle, probably reflecting the amount of food-intake and the composition of the energy stores which are being built up (Jenni and Jenni-Eiermann 1996). According to our analyses, short-term fasted birds decreased triglyceride levels by a constant amount, regardless of whether the birds had high (migratory period) or medium (molting period) triglyceride levels. However, Blackcaps in the postbreeding period reduced triglyceride levels to a lesser extent than in the molting and migratory period, possibly because their low triglyceride levels cannot be reduced much further.

Free fatty acid levels of feeding Blackcaps also showed differences between the three pe-

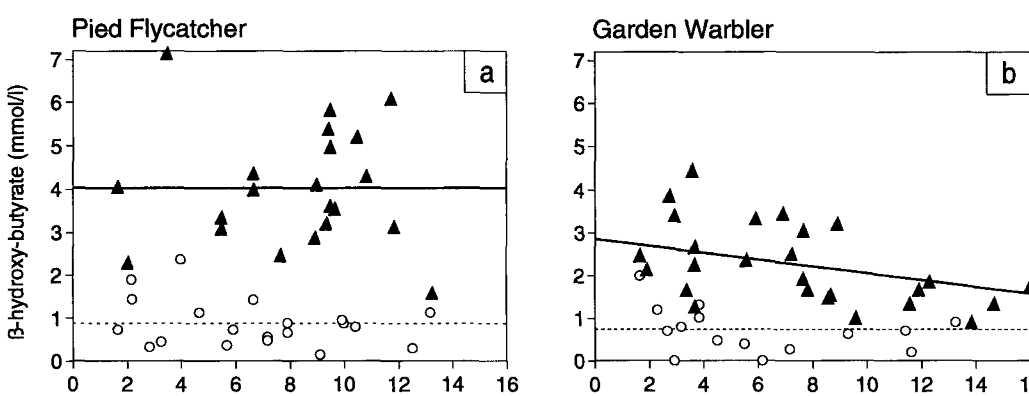

FIGURE 3. Regression of plasma β-hydroxy-butyrate concentrations upon time after dawn in (a) Pied Flycatchers during the migratory period and (b) Garden Warblers during the migratory period. See Figure 1 for explanations and Tables 2 and 4 for regression model.

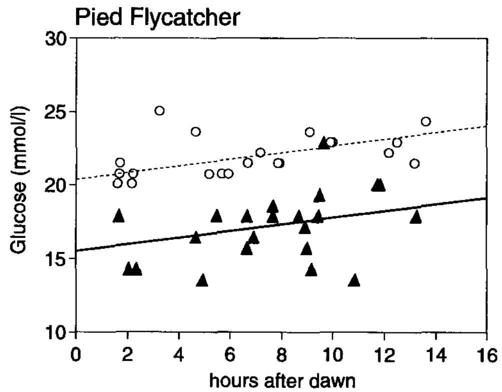

FIGURE 4. Regression of plasma glucose concentrations upon time after dawn in Pied Flycatchers during the migratory period. See Figure 1 for explanations and Table 4 for regression model.

riods of the annual cycle. However, short-term fasted Blackcaps increased free fatty acid levels by a similar amount in each period.

β-hydroxy-butyrate levels of feeding birds exhibited no significant differences between the three periods of the annual cycle. Short-term fasted Garden Warblers in the migratory period increased β-hydroxy-butyrate levels to a smaller extent than in the molting period. This may be due to the higher reservoir of food and plasma triglycerides in birds during the migratory period which is used during part of the fasting time. However, this difference was not observed in the Blackcap. Glucose and uric acid levels exhibited little difference between the three periods of the annual cycle.

In summary, the period of the annual cycle has little influence on the metabolic response to short-term fasting during the day, although birds in the postbreeding period with their low lipid reserves may rely less on plasma triglycerides.

DEPENDENCE ON TIME OF DAY

For the metabolites examined, only a few diurnal trends (slopes) were significantly different between feeding and short-term fasted birds. The most important difference was found in β-hydroxy-butyrate: the levels of feeding birds decreased very rapidly in the very early morning and remained stable thereafter (Jenni and Jenni-Eiermann 1996), while the levels of short-term fasted birds decreased continuously over the day in all species except the Pied Flycatcher. Hence, short-term fasted birds synthesize less β-hydroxy-butyrate with progressing time of day. This probably is due to the availability of more dietary energy substrates with progressing time of day. Indeed, plasma triglyceride levels increase during the course of the day, especially in the morning (Jenni and Jenni-Eiermann 1996), and these elevated levels of triglycerides have been suggested to be an important energy substrate during overnight fasting (Jenni-Eiermann and Jenni 1996). Compared with the other species, Pied Flycatchers exhibit a more moderate increase in triglyceride levels during the whole day which is correlated with a foraging activity more evenly distributed over the entire daylight hours (Jenni and Jenni-Eiermann 1996). Hence, in the Pied Flycatcher energy accumulation from the diet can be expected to be less rapid and less concentrated in the early morning than in the other species. This may explain the absence of decreasing β-hydroxy-butyrate levels in short-term fasted Pied Flycatchers.

Plasma triglyceride levels were examined only after the steep early morning increase and were shown to increase in parallel in feeding and short-term fasted birds. However, in the early morning triglyceride levels of feeding and short-term fasted birds are likely to be similarly low. Thus, in the early morning, short-term fasting may decrease plasma triglyceride levels less than later on, because lipid production from the diet has not yet started.

Contrary to the other species and contrary to feeding conspecifics, short-term fasted Garden Warblers displayed decreasing free fatty acid and glycerol levels and increasing uric acid levels during the day. This pattern was consistent only in molting birds. It may indicate that these birds reduce the mobilization of lipids from adipose tissues during the course of the day at the expense of protein.

In summary, the metabolic response to short-term fasting is modified during the course of the day. In the early morning, when glycogen reserves are depleted (Swain 1991), fasting birds apparently mobilize their fat reserves to synthesize β-hydroxy-butyrate to partly replace glucose and they cannot rely on plasma triglycerides from the diet. During the morning, food-intake increases, glycogen reserves are restored and the reliance on β-hydroxy-butyrate decreases during short-term fasting. After the first hours of the daylight period, short-term fasted birds apparently rely on plasma triglycerides from the diet and on lipids from adipose tissues at a similar rate throughout the day. However, results for molting Garden Warblers indicate that some birds may decrease their reliance on lipids and use more protein with progressing time of day.

RECOGNITION OF SHORT-TERM FASTED BIRDS IN FIELD STUDIES

The present study indicates that metabolite levels may be used to distinguish normally feeding from short-term fasted birds. In this study, the birds caught during the day and blood-sampled within 20 min were all assumed to be normally fed. Preliminary analyses, however, indicated that certain metabolite levels correlate with the prevailing weather, suggesting that not all birds were equally well-fed. Hence, the differences between well-fed and short-term fasted birds may actually be larger than reported in this study.

In order to use metabolite levels as indicators of short-term fasting in field studies, several points need to be observed. Since metabolite levels may vary between species and may depend on the period of the annual cycle (see Jenni and Jenni-Eiermann 1996, Jenni-Eiermann and Jenni 1996), a control sample of well-fed conspecifics in the same period of the annual cycle is needed. Among the metabolites examined, triglycerides and β-hydroxy-butyrate showed the largest and most consistent differences between feeding and short-term fasted birds. These two metabolites also were the ones which correlated best with the change in body mass in captive Garden Warblers fed different amounts of food (Jenni-Eiermann and Jenni 1994). When using β-hydroxy-butyrate to recognize short-term fasted birds, the dependence of the reaction to short-term fasting on time of day also has to be taken into account. In the case of β-hydroxy-butyrate and triglycerides, there are probably no or only small differences between feeding and short-term fasted birds in the early morning.

ACKNOWLEDGMENTS

We thank U. Andres for carrying out the glucose determinations, H. P. von Hahn, Stiftung für Experimentelle Altersforschung, for giving us laboratory equipment, and all persons helping at the ringing stations and enduring our special wishes.

LITERATURE CITED

CHEREL, Y., AND Y. LE MAHO. 1988. Changes in body mass and plasma metabolites during short-term fasting in the King Penguin. Condor 90:257–258.

CHEREL, Y., J.-P. ROBIN, AND Y. LE MAHO. 1988. Physiology and biochemistry of long-term fasting in birds. Can. J. Zool. 66:159–166.

ELIA, M., C. ZED, G. NEALE, AND G. LIVESEY. 1987. The energy cost of triglyceride-fatty acid recycling in non-obese subjects after an overnight fast and four days of starvation. Metabolism 36:251–255.

HAVEL, R. J. 1987. Lipid transport function of lipoproteins in blood plasma. Am. J. Physiol. 253:E1–E5.

HURLEY, B. F., P. M. NEMETH, W. H. MARTIN III, J. M. HAGBERG, G. P. DALSKY, AND J. O. HOLLOSZY. 1986. Muscle triglyceride utilization during exercise: effect of training. J. Appl. Physiol. 60:562–567.

JENNI, L., AND S. JENNI-EIERMANN. 1992. Metabolic patterns of feeding, overnight fasted and flying night migrants during autumn migration. Ornis Scand. 23:251–259.

JENNI. L., AND S. JENNI-EIERMANN. 1996. Metabolic responses to diurnal feeding patterns during the postbreeding, moulting, and migratory period in passerine birds. Funct. Ecol. 10:73–80.

JENNI-EIERMANN, S., AND L. JENNI. 1991. Metabolic responses to flight and fasting in night migrating passerines. J. Comp. Physiol. B 161:465–474.

JENNI-EIERMANN, S., AND L. JENNI. 1994. Plasma metabolite levels predict individual body-mass changes in a small long-distance migrant, the Garden Warbler. Auk 111:886–897.

JENNI-EIERMANN, S., AND L. JENNI. 1996. Metabolic differences between the postbreeding, moulting and migratory periods in feeding and fasting passerine birds. Funct. Ecol. 10:62–72.

KLEIN, S., O. B. HOLLAND, AND R. R. WOLFE. 1990. Importance of blood glucose concentration in regulating lipolysis during fasting in humans. Am. J. Physiol. 258:E32–E39.

LINDGÅRD, K., K. A. STOKKAN, Y. LE MAHO, AND R. GROSCOLAS. 1992. Protein utilization during starvation in fat and lean Svalbard Ptarmigan (*Lagopus mutus hyperboreus*). J. Comp. Physiol. B 162:607–613.

MORI, J. G., AND J. C. GEORGE. 1978. Seasonal changes in serum levels of certain metabolites, uric acid and calcium in the migratory Canada Goose (*Branta canadensis interior*). Comp. Biochem. Physiol. 59B:263–269.

ROBIN, J.-P., Y. CHEREL, H. GIRARD, A. GELOEN, AND Y. LE MAHO. 1987. Uric acid and urea in relation to protein catabolism in long-term fasting geese. J. Comp. Physiol. B 157:491–499.

ROBINSON, D. S. 1970. The function of the plasma triglycerides in fatty acid transport, p. 51–105. *In* M. Florkin and E. H. Stotz [eds.], Comprehensive biochemistry. Vol. 18. Elsevier, Amsterdam.

ROBINSON, A. M., AND D. H. WILLIAMSON. 1980. Physiological roles of ketone bodies as substrates and signals in mammalian tissues. Physiol. Rev. 60:143–187.

SCOW, R. O., AND S. S. CHERNICK. 1970. Mobilization, transport, and utilization of free fatty acids, p. 19–50. *In* M. Florkin and E. H. Stotz [eds.], Comprehensive biochemistry. Vol. 18. Elsevier, Amsterdam.

SWAIN, S. D. 1987. Overnight changes in circulating energy substrate concentrations in the Vesper Sparrow (*Pooecetes gramineus*). Comp. Biochem. Physiol. 86A:439–441.

SWAIN, S. D. 1991. Metabolism and energy reserves of brood-rearing Horned Larks (*Eremophila alpestris*). Comp. Biochem. Physiol. 99A:69–73.

SWAIN, S. D. 1992. Energy substrate profiles during fasting in Horned Larks (*Eremophila alpestris*). Physiol. Zool. 65:568–582.