The Auk 116(4):994–1000, 1999

PLASMA LIPID METABOLITES PROVIDE INFORMATION ON MASS CHANGE OVER SEVERAL DAYS IN CAPTIVE WESTERN SANDPIPERS

TONY D. WILLIAMS,[1] CHRISTOPHER G. GUGLIELMO, OLIVER EGELER, AND CHRISTOPHER J. MARTYNIUK

Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada

ABSTRACT.—Individual quality is often assessed using a static measure of body condition, such as size-corrected body mass. Plasma metabolites have the potential to provide information on the dynamics of physiological state and thus may be better measures of individual performance capacity (and fitness). We studied relationships between rate of mass change and circulating levels of triglycerides, glycerol, and β-hydroxybutyrate in captive Western Sandpipers (*Calidris mauri*). The rate of mass change over one and two days prior to blood sampling was positively related to residual triglyceride (controlling for body mass at sampling) and negatively related to residual glycerol and residual β-hydroxybutyrate. The relationship between metabolite level and mass change was still apparent over a seven-day interval for glycerol, but not for the other two metabolites. In a stepwise multiple regression of mass change over two days (controlling for body mass), only β-hydroxybutyrate and glycerol were entered in the model at $P < 0.15$. Analysis of group means for seven sampling events showed that body-mass change in a group of individuals was related to mean circulating levels of each metabolite, i.e. to a characteristic metabolite profile. Thus, it may be feasible to employ these metabolites to assess habitat quality based on animal performance (e.g. at migratory stopover sites), or to understand the effects of climatic or anthropogenic factors on the health and survival of animals. *Received 19 May 1998, accepted 8 February 1999.*

INDIVIDUAL QUALITY (variation in body condition or "health") is a widely used concept in behavioral and ecological studies. Body condition perhaps is most simply defined as the degree to which an organism's physiological state influences its performance (e.g. production or activity; Brown 1996), which, in turn, is assumed to be positively related to fitness (sensu Arnold 1983). Traditionally, measures of condition have been based on some aspect of body composition, such as nutrient reserves. More recently, studies have attempted to use a wide range of physiological measures of condition that are not directly based on nutrient reserves, including plasma metabolites (Andersson and Gustaffson 1995, Dawson and Bortolotti 1997), glucocorticoids (Wingfield et al. 1992), hematocrit (Piersma et al. 1996), and immune-system function (Lochmiller et al. 1993, Ots and Hôrak 1996).

In almost all cases, compositional, morphological, or physiological indices of body condition or quality provide only a static assessment of the individual at a single point in time, usually the time of capture. This might be a major problem if two individuals (or two sampled populations) are undergoing rapid changes in condition. For example, two individuals could have the same condition index or body mass at capture, leading to the conclusion that they are of equal quality (and predicted fitness). However, one individual might be on a trajectory of rapid mass loss, whereas the mass of a second individual might be constant or increasing over time. In reality, the former individual would be of lower quality than the latter individual. Physiological indices of condition or quality are much more valuable if they provide information on the dynamics or rate and direction of change in condition over time.

Recently, Jenni-Eiermann and Jenni (1994) reported that several plasma metabolites (in particular, triglyceride and β-hydroxybutyrate) could predict individual mass change over several hours in captive Garden Warblers (*Sylvia borin*), which are small migratory passerines. In this paper, we show that plasma lipid metabolites (triglycerides, glycerol, and β-hydroxybutyrate) can provide information on rates of

[1] E-mail: tdwillia@sfu.ca

TABLE 1. Details of body mass ($\bar{x} \pm$ SE) in experimental Western Sandpipers at the start and end of sampling periods. Mass change in birds from samples 5 to 7 was experimentally induced via short-term food deprivation.

Sample	Date	Body mass (g)		Rate (g/day)	No. days	No. birds
		Start	End			
1	18 January	25.2 ± 1.1	25.9 ± 1.2	0.31 ± 0.11	2	13
2	20 February	33.1 ± 1.4	34.0 ± 1.6	0.13 ± 0.08	7	17
3	3 April	34.2 ± 0.9	31.7 ± 0.8	−0.36 ± 0.08	7	16
4	12 July	34.2 ± 1.5	29.8 ± 1.1	−2.16 ± 0.32	2	14
5	3 & 29 November	22.6 ± 0.6	20.1 ± 0.5	−2.41 ± 0.27	1	12
6	4 November	21.1 ± 0.7	23.7 ± 0.5	1.31 ± 0.24	2	6
7	30 November	23.0 ± 0.7	25.1 ± 0.8	2.13 ± 0.20	1	6

mass change in captive Western Sandpipers (*Calidris mauri*) over time periods up to at least two days (48 h). We also illustrate how plasma metabolite profiles may be used to determine mass-change trajectories of different sample populations of birds, e.g. from different habitats or relative to different climatic conditions or anthropogenic disturbances.

METHODS

Experimental protocol.—Juvenile Western Sandpipers were captured in mist nets during southward migration in August 1994 and 1995 at Boundary Bay in British Columbia, Canada (49°10′N, 123°05′W). Animal handling protocols conformed with Canadian Committee for Animal Care guidelines, and birds were captured and maintained under permits from Canadian Wildlife Service, Environment Canada, and Simon Fraser University Animal Care Committee. Birds were maintained in groups of 12 to 16 in outdoor pens (3 × 6 m) on natural day lengths, with food (Clark's trout chow) and water provided *ad libitum*. Infrared heating lamps were provided during winter months, and experiments began a minimum of three months after capture. Mass change and plasma metabolite data were obtained from two experimental groups of sandpipers for a total of seven sampling periods (see Table 1): (1) natural mass change (n = 17 birds, 4 sample periods), in which birds were weighed at either two or seven days before blood sampling; and (2) experimentally induced mass change (n = 12 birds, 3 sample periods), in which mass change was induced by short-term food deprivation (24 h) and re-feeding. The birds in group 2 were different from those in group 1, and we sampled their blood after one or two days of mass change. Birds were captured one at a time and sampled indoors away from the pens such that individuals not being sampled were left undisturbed to feed, bathe, etc. For all birds, blood was sampled from the brachial vein between 0930 and 1130 PST (to control for possible diurnal variation in metabolite levels). Time from capture to blood sampling was less than 3 min in all cases. Blood (up to 200 μL) was collected in heparinized capillary tubes, transferred to 0.6-mL Eppendorf tubes, and centrifuged at 5,000 rpm (2,200 × g) for 10 min. Plasma was stored at −20°C until further analysis. We present pooled data from the two experiments on plasma metabolite concentrations and body mass at the time of blood sampling relative to the rate of mass change before sampling at intervals of one, two, and seven days.

Metabolite assays.—Plasma triglycerides and glycerol were measured with enzymatic endpoint assays (Wako Diagnostics, Richmond, and Sigma), and plasma β-hydroxybutyrate was measured by enzymatic assay (Sigma). We followed manufacturers' protocols except that the assays were modified for use with small volumes of plasma (5 μL) using 96-well microplates, with assays being read on a Biotek 340i microplate reader. Samples were assayed in triplicate. Because the triglyceride assay also measured free glycerol, true plasma triglyceride levels were calculated by subtracting glycerol from total triglyceride. Assays were validated using reference values from normal and abnormal human control sera (Wako). Coefficients of variation between assays were 6.2% (n = 11), 8.1% (n = 5), and 18.1% (n = 8) for triglyceride, glycerol, and β-hydroxybutyrate, respectively. Small volumes of plasma precluded us from assaying for all three metabolites in some samples, so sample sizes vary.

Statistical analysis.—All plasma metabolite data were distributed non-normally (Shapiro-Wilk's test, $P < 0.05$), so we transformed the data using ln(metabolite + 0.5). Data were analyzed in two ways. First, at the level of the individual, we compared rates of mass change with plasma levels of each of the three metabolites over three time intervals (one, two, and seven days) using multiple regression analysis (to control for the effect of body mass at the time of sampling). To avoid pseudoreplication we randomly selected a single record for each individual bird for each time interval from one of the seven total sampling periods. Second, in a

population level analysis, we compared the mean rate of mass change for each sampling period with mean plasma metabolite levels for the seven sampling periods using Spearman rank correlation. We considered that this second analysis more closely approximated the situation that would occur in the field where data would be obtained from several groups of individuals (e.g. at different times or in different habitats) with a variable and unknown period of mass change prior to capture and blood sampling. We had *a priori* expectations of directional relationships between metabolites and mass change, so we used one-tailed statistical tests. All values are given as $\bar{x} \pm$ SE unless otherwise stated.

RESULTS

Absolute body mass and the rate of mass change varied widely among sampling periods; data on body mass at the start and end of the period of mass change, rate of mass change, and the time interval for each sampling period are given in Table 1. Plasma β-hydroxybutyrate concentrations were negatively correlated with triglyceride ($r = -0.53$, $n = 50$, $P < 0.001$) and positively correlated with glycerol ($r = 0.43$, $n = 50$, $P < 0.002$) among individual birds. Plasma triglyceride and glycerol concentrations were not significantly correlated ($r = 0.11$, $n = 66$, $P > 0.30$). Plasma triglyceride levels were positively related to body mass at the time of blood sampling ($F = 65.5$, df = 1 and 37, $r^2 = 0.64$, $P < 0.001$), whereas plasma β-hydroxybutyrate levels were negatively related to body mass ($F = 5.70$, df = 1 and 31, $r^2 = 0.21$, $P < 0.01$). Regression equations for these relationships were:

$$\text{triglyceride} = 0.06(\text{mass}) - 1.12 \quad (1)$$

and

$$\beta\text{-hydroxybutyrate} = -0.04(\text{mass}) + 1.96. \quad (2)$$

Plasma glycerol concentration was independent of body mass for our data set ($F = 0.04$, df = 1 and 37, $P > 0.80$). Nonetheless, we controlled for body mass in subsequent analyses for all three plasma metabolites (which did not affect any of our results or conclusions).

Rates of mass change in individual birds were positively related to plasma triglyceride at the time of blood sampling for the one-day ($F = 3.93$, df = 1 and 10, $P = 0.04$) and the two-day ($F = 12.09$, df = 1 and 19, $P < 0.01$; Fig. 1) sampling intervals, but not for mass change over seven days ($F = 0.07$, df = 1 and 13, $P > 0.80$). The equation for the relationship between mass change and mass-corrected triglyceride for the two-day interval, for which we had the largest sample size, was:

$$\text{mass change} = 7.61(\text{triglyceride}) - 0.05. \quad (3)$$

Mass change over two days was negatively related to plasma glycerol ($F = 27.98$, df = 1 and 19, $r^2 = 0.61$, $P < 0.001$; Fig. 1) and β-hydroxybutyrate ($F = 26.71$, df = 1 and 18, $r^2 = 0.61$, $P < 0.001$; Fig. 1). The equations for the relationships between mass change and mass-corrected metabolite concentrations for these data were:

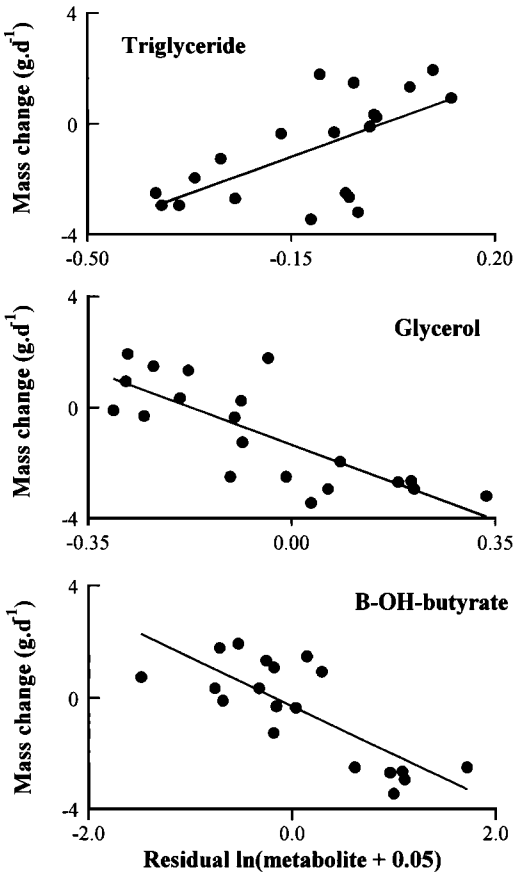

FIG. 1. Relationship between individual rate of body-mass change within two days of blood sampling and levels of plasma triglyceride ($n = 20$), glycerol ($n = 20$) and β-hydroxybutyrate ($n = 19$) in captive Western Sandpipers. Metabolite concentrations (mmol per L) are residuals from the regression with body mass.

$$\text{mass change} = -7.77(\text{glycerol}) - 1.34 \quad (4)$$

and

$$\text{mass change} = -1.74(\beta\text{-hydroxybutyrate}) - 0.30. \quad (5)$$

Plasma glycerol levels were also negatively related to mass change over one day ($F = 9.37$, df = 1 and 10, $r^2 = 0.51$, $P < 0.025$), and this relationship was still apparent over seven days ($F = 24.71$, df = 1 and 13, $r^2 = 0.67$, $P < 0.001$). The level of β-hydroxybutyrate was similarly related to mass change over one day ($F = 4.22$, df = 1 and 9, $P = 0.035$) but not over seven days ($F = 0.23$, df = 1 and 12, $P > 0.60$).

In a stepwise multiple regression of mass change over two days in which residual triglyceride, glycerol, and β-hydroxybutyrate were entered as independent variables (controlling for body mass), only β-hydroxybutyrate (partial $r^2 = 0.54$, $P < 0.001$) and glycerol (partial $r^2 = 0.10$, $P < 0.05$) entered into the model at $P < 0.15$ ($n = 20$).

Analysis of group means for the seven sampling periods showed a similar overall pattern to the analysis at the individual level (Fig. 2): rate of mass change was positively correlated with the residual level of plasma triglyceride ($r_s = 0.857$, $P < 0.025$) and negatively correlated with residual levels of plasma glycerol ($r_s = -0.786$, $P < 0.05$) and plasma β-hydroxybutyrate ($r_s = -0.898$, $P < 0.01$).

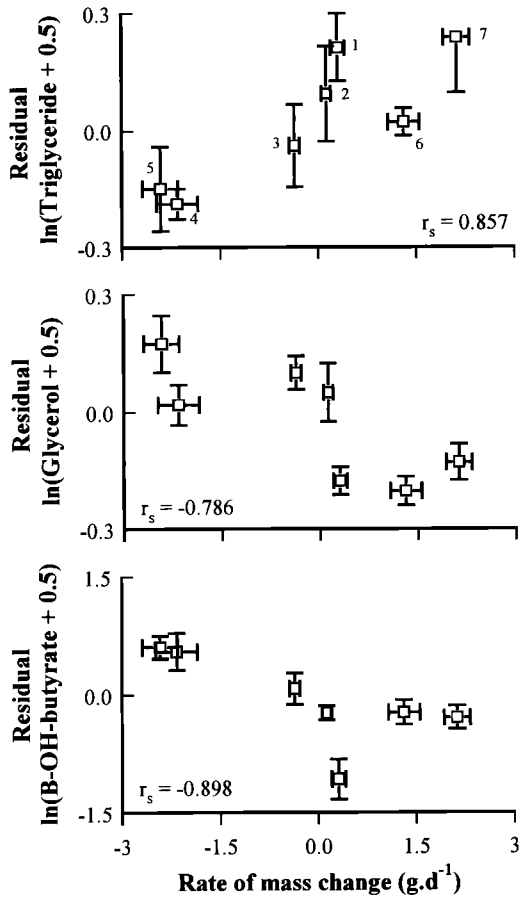

FIG. 2. Relationship between average rate of mass change in captive Western Sandpipers and mean levels of plasma triglyceride, glycerol, and β-hydroxybutyrate for each sampling event ($n = 7$). Metabolite concentrations (mmol per L) are residuals from the regression with body mass. Numbers refer to sampling events (see Table 1).

DISCUSSION

Jenni-Eiermann and Jenni (1994) showed that plasma metabolites could provide information on rates of body-mass change over a few hours in a small migratory passerine. Our results with Western Sandpipers extend this technique and clearly demonstrate that certain plasma metabolites can be used to provide information on rates of mass change *before* a capture and blood sampling event in individual birds over a period of at least two days. Lengths of stay at stopover sites during migration average three to four days in the Western Sandpiper (Warnock and Bishop 1997), so analysis of plasma metabolites can predict mass change for biologically relevant time intervals in this species. In addition, rate of mass change, which largely reflects rate of fat deposition (Lindström and Piersma 1993, C. Guglielmo unpubl. data), is a very important predictor for migratory success, and condition assessed using plasma metabolites should therefore be directly related to an organism's performance. Plasma triglycerides increased with increasing mass gain, whereas glycerol and β-hydroxybutyrate increased with increasing mass loss, consistent with known physiological functioning of these metabolites. During fat deposition, triglycerides increase in the plasma owing to transport of lipids to peripheral adipose tissue, either directly from the gut (as portomicrons) or indirectly via the liver as very low-density lipoproteins (Robinson 1970, Ramenofsky 1990). During mass loss (i.e. when birds are in negative

energy balance), glycerol and free fatty acids (FFA) are released into the plasma during lipolysis of triglycerides in adipose tissue, and β-hydroxybutyrate (a ketone body) is synthesized from FFA, replacing glucose as the principal fuel for respiration in some tissues (Ramenofsky 1990, Horton et al. 1993). Thus, glycerol and β-hydroxybutyrate increase in the plasma during mass loss, which is indicative of lipid catabolism and glucose shortage (Jenni-Eiermann and Jenni 1994).

Although we report an experimental study using captive birds provided with artificial food, we see no reason why the same general relationship(s) between mass change and plasma metabolite levels should not occur in free-living birds, because mass changes in captivity and in the wild should involve a common physiological mechanism and thus give rise to similar changes in plasma biochemistry (Cherel et al. 1988a). However, our data should be extrapolated to free-living birds with caution, particularly with regard to mass change over the longer seven-day interval. Plasma levels of all three metabolites reflected mass change over one and two days, but these relationships were less consistent over the seven-day interval. It is possible that plasma metabolite profiles simply reflect instantaneous rates of mass change, or change over very short time intervals (i.e. one-half to one day). Assuming that mass change is linear, any relationship between changes in mass over longer time intervals would then be due to the effect of the single most-recent day. Our experimental protocol meant that mass change in our birds was more or less constant and linear; e.g. mass change over two days before blood sampling was highly correlated with mass change two days after sampling (T. D. Williams unpubl. data). This may not be the case under certain circumstances in free-living birds (e.g. with marked diurnal fluctuations in mass in small passerines; Meijer et al. 1994, Witter et al. 1995), although several studies suggest that rapid mass gain during fat deposition is approximately linear and constant in migratory shorebirds over several days (Zwarts et al. 1990, Lindström 1991). Thus, the relationship between glycerol and mass change that we report for the seven-day interval may be an artifact of our particular experimental design. However, we do not believe that this is entirely the case. If metabolite levels reflected only instantaneous (i.e. short-term) mass change, then we would have predicted more consistent relationships between metabolites and mass change regardless of the time interval used (given that mass change was linear). In fact, of the three metabolites measured, only glycerol was still related to mass change over the longer (seven day) interval. This suggests that certain metabolites indeed "integrate" information on physiological state over several days, in addition to reflecting short-term changes in mass. For example, in long-term-fasting penguins, concentrations of plasma β-hydroxybutyrate and urea increase throughout stage II of fasting (protein sparing; Cherel et al. 1988b), even though mass loss is constant at this time (Cherel et al. 1988a). Thus, in this case absolute metabolite concentrations reflect both the rate and the duration of mass loss. Some support exists for this interpretation of our data in that glycerol was the only metabolite we measured that was not related to body mass at the time of blood sampling; i.e. plasma glycerol appeared to be less dependent on the bird's current physiological state than were triglyceride and β-hydroxybutyrate.

Another potential difference between our experimental study and that for free-living birds is that some of our birds gained and lost mass at relatively high rates (up to 2 g per day). Zwarts et al. (1990) predicted maximum rates of increase in mass of 4 to 5% of "winter" mass per day, using data on fat deposition from 42 studies of shorebirds. This would represent 1.1 g per day for a 22.7-g Western Sandpiper. Similarly, Lindström (1991) gave a range of maximum fat deposition rates of 2.6 to 4.3% of lean mass, i.e. 0.59 to 0.98 g per day for a 22.7-g Western Sandpiper. Maximum rates of fat deposition reported for congeneric Semipalmated Sandpipers (*C. pusilla*) are 1.1 to 1.26 g per day (Lank 1983, White 1985). However, in our study the relationship between mass change over the seven-day interval and plasma glycerol occurred over a range of mass changes of ±1 g per day, which is within the range reported for field studies. Furthermore, for the population-level analysis, the relationship between rate of mass change and plasma metabolites was still apparent within the range of ±1.5 g per day, especially for plasma triglyceride (see Fig. 2).

Similarities and important differences exist between our study and that of Jenni-Eiermann

and Jenni (1994). In the latter study, β-hydroxybutyrate and triglyceride together explained 61% of the total variation in body-mass change, with partial r^2-values of 51% and 44%, respectively. Jenni-Eiermann and Jenni (1994:table 4) did not find a significant relationship between mass change and plasma glycerol in a multiple regression analysis. Variation in rate of mass change in captive Western Sandpipers over two days was significantly related to plasma levels of all three metabolites, but glycerol and β-hydroxybutyrate were better at explaining variation (each 61%) than was triglyceride (40%). In the multiple regression analysis, β-hydroxybutyrate was entered first into the model, suggesting that it was the single best predictor of mass change over two days, which is consistent with the finding of Jenni-Eiermann and Jenni (1994). It is unclear whether the difference between our results and those of Jenni-Eiermann and Jenni (1994) with regard to glycerol reflects a species-specific effect or suggests that different metabolites are more or less useful in predicting mass change over varying time intervals (hours versus days; see above). Nevertheless, our results suggest that glycerol is an important predictor of mass change and that levels of triglyceride and glycerol should be reported separately in future studies. In a more recent study, Jenni-Eiermann and Jenni (1997: 114) reported triglyceride values including free glycerol, stating that "glycerol values were low compared with triglyceride values." At least in the Western Sandpiper, this is not the case, because glycerol can represent a substantial (and variable) proportion of total triglyceride (30% in free-living birds; C. Guglielmo unpubl. data).

Although plasma metabolites can provide information on individual rates of body-mass change over several days, this technique might also be applied to comparisons among populations sampled at different points in time, in different habitats, or during different activities (see Jenni-Eiermann and Jenni 1996). Our study provides an excellent example of the value of using a physiologically realistic technique to assess condition in such a situation. Compare, for example, our sampling periods 1 and 4 (both sampled over two days and from the natural mass-change experiment). Mean body mass for the birds in these two "sampling populations" was 25.9 g and 29.8 g, respectively, at the time of blood sampling. Using conventional measures of condition, birds in sample 4 would likely have been characterized as being in better condition than birds in sample 1. However, birds in sample 4 were on a steep trajectory of mass loss compared with birds in sample 1, which were maintaining more or less constant mass. This difference in mass change was clearly revealed by the metabolite profiles of these two samples of birds, with birds in sample 4 being characterized by high β-hydroxybutyrate and glycerol levels and low triglyceride levels compared with birds in sample 1 (Fig. 2). The use of such metabolite profiles to compare the physiological state and mass-change trajectory of different subpopulations of birds might represent the most useful application of this technique to conservation and management, for example in assessing the health of populations in relation to habitat quality or anthropogenic factors. However, studies that examine the factors that influence variability in the levels of these metabolites in free-living birds (e.g. time of day, tidal cycle, and temperature) are needed.

Literature Cited

Andersson, M. S., and L. Gustaffson. 1995. Glycosylated haemoglobin: A new measure of condition in birds. Proceedings of the Royal Society of London Series B 260:299–303.

Arnold, S. J. 1983. Morphology, performance and fitness. American Zoologist 23:347–361.

Brown, M. E. 1996. Assessing body condition in birds. Current Ornithology 13:67–135.

Cherel, Y., J.-P. Robin, and Y. Le Maho. 1988a. Physiology and biochemistry of long-term fasting in birds. Canadian Journal of Zoology 66: 159–166.

Cherel, Y., J.-P. Robin, O. Walche, H. Karmann, P. Netchitailo, and Y. Le Maho. 1988b. Fasting in King Penguins I. Hormonal and metabolic changes during breeding. American Journal of Physiology 254:R170–177.

Dawson, R. D., and G. R. Bortolotti. 1997. Total plasma protein levels as an indicator of condition in wild American Kestrels (*Falco sparverius*). Canadian Journal of Zoology 75:680–686.

Horton, H. R., L. A. Moran, R. S. Ochs, J. D. Rawn, and K. G. Scrimgeour. 1993. Principles of biochemistry. Prentice-Hall, Englewood Cliffs, New Jersey.

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 111:888–899.

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

JENNI-EIERMANN, S., AND L. JENNI. 1997. Diurnal variation of metabolic responses to short-term fasting in passerine birds during the postbreeding, molting and migratory period. Condor 99:113–122.

LANK, D. B. 1983. Migratory behavior of Semipalmated Sandpipers at inland and coastal staging areas. Ph.D. thesis, Cornell University, Ithaca, New York.

LINDSTRÖM, Å. 1991. Maximum fat deposition rates in migrating birds. Ornis Scandinavica 22:12–19

LINDSTRÖM, Å., AND T. PIERSMA. 1993. Mass changes in migrating birds: The evidence for fat and protein storage re-examined. Ibis 135:70–78.

LOCHMILLER, R. L., M. R. VESTEY, AND J. C. BOREN. 1993. Relationship between protein nutritional status and immunocompetence in Northern Bobwhite chicks. Auk 110:503–510.

MEIJER, T., F. J. MOHRING, AND F. TRILLMICH. 1994. Annual and daily variation in body mass and fat of Starlings *Sturnus vulgaris*. Journal of Avian Biology 25:98–104.

OTS, A., AND P. HÖRAK. 1996. Great Tits *Parus major* trade health for reproduction. Proceedings of the Royal Society of London Series B 263:1443–1447.

PIERSMA, T., J. M. EVERAARTS, AND J. JUKEMA. 1996. Build-up of red blood cells in refuelling Bartailed Godwits in relation to individual migratory quality. Condor 98:363–370.

RAMENOFSKY, M. 1990. Fat storage and fat metabolism in relation to migration. Pages 214–231 *in* Bird migration: Physiology and ecophysiology (E. Gwinner, Ed.). Springer-Verlag, Berlin.

ROBINSON, D. S. 1970. The function of the plasma triglycerides in fatty acid transport. Comprehensive Biochemistry 18:51–105.

WARNOCK, N., AND M. A. BISHOP. 1997. Spring stopover ecology of migrant Western Sandpipers. Condor 100:456–467.

WHITE, L. M. 1985. Body composition and fat deposition of migrant Semipalmated Sandpipers during autumn migration in the Bay of Fundy. M.S. thesis, University of Guelph, Guelph, Ontario.

WINGFIELD, J. C., C. M. VLECK, AND M. C. MOORE. 1992. Seasonal changes of the adrenocortical response to stress in birds of the Sonoran Desert. Journal of Experimental Zoology 264:419–428.

WITTER, M. S., J. P. SWADDLE, AND I. C. CUTHILL. 1995. Periodic food availability and strategic regulation of body mass in the European Starling. Functional Ecology 9:568–574.

ZWARTS, L., B. J. ENS, M. KERSTEN, AND T. PIERSMA. 1990. Moult, mass, and flight range of waders ready to take off for long-distance migrations. Ardea 78:339–364.

Associate Editor: A. J. Baker