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EXTRINSIC AND INTRINSIC SOURCES OF VARIATION IN PLASMA LIPID METABOLITES OF FREE-LIVING WESTERN SANDPIPERS (*CALIDRIS MAURI*)

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ABSTRACT.—Plasma lipid metabolites may be useful indicators of mass changes in migratory birds. To test utility of plasma metabolites in field studies, we examined effects of several extrinsic (bleed time, time of day, location) and intrinsic (body mass, sex, age, migratory state) factors on plasma concentrations of triglycerides (TRIG), glycerol (GLYC), and B-OH-butyrate (BUTY) in free-living Western Sandpipers (*Calidris mauri*). TRIG and GLYC decreased rapidly following capture (2–20 min), whereas BUTY did not change. GLYC and BUTY were negatively correlated to body mass. TRIG was positively correlated to body mass in migrant females, but not consistently in migrant males, or in females captured on the wintering grounds. Taking into account other sources of variation, the two measures of lipid utilization (GLYC and BUTY) varied little through the year. TRIG showed the greatest potential for use in field studies. TRIG was lowest during winter, when birds were leanest, and highest during spring and fall migration, when sandpipers were gaining mass rapidly at stopovers. TRIG differed between sandpipers refuelling a two stopover sites separated by 35 km, demonstrating that populations of birds can have characteristic lipid metabolite profiles that may reflect local differences in fattening rate. *Received 12 February 2001, accepted 12 December 2001.*

RESUMEN.—Los metabolitos lipi

Gustafsson 1995; Brown 1996; Jenni and Jenni-Eiermann 1996; Dawson and Bertolotti 1997; Gannes 1999). Nevertheless, reliable interpretation of blood assays requires an understanding of how factors like stress, body mass, age, and sex affect baseline metabolite levels. Whereas these methods have been validated in humans and domestic animals, knowledge of the many possible sources of variation in wild animals remains rudimentary.

Studies with captive birds indicate that plasma lipid metabolites can be used to measure mass change at the individual or population level. Mass gain from morning to mid-day related positively to plasma triglyceride and negatively to B-OH-butyrate levels in Garden Warblers (*Sylvia borin*; Jenni-Eiermann and Jenni 1994). These same relationships were found in captive Western Sandpipers (*Calidris mauri*), and in addition, plasma glycerol was negatively correlated with rate of mass gain (Williams et al. 1999). At the individual level, determining rate and direction of mass change may provide a measure of physiological performance (fitness). At the population level, lipid metabolite profiles could be used to compare rates of mass gain at different sites, and thus provide an index of habitat quality based on animal performance (Jenni and Jenni-Eiermann 1996, Williams et al. 1999). Field studies of day-feeding passerines seem to support the use of lipid metabolites in that manner (Jenni and Jenni-Eiermann 1996, Jenni-Eiermann and Jenni 1996, Schaub and Jenni 2001). It is unclear if the technique can be applied easily to species like shorebirds, whose feeding may be related to both light and tide conditions.

In this study, we examined effects of several extrinsic (bleed time, time of day, site) and intrinsic (body mass, sex, age, migratory state) factors on plasma concentrations of triglycerides (TRIG), glycerol (GLYC), and B-OH-butyrate (BUTY) in Western Sandpipers. This shorebird migrates long distances between Arctic breeding areas and wintering grounds located mainly along the Pacific coast of the Americas (Wilson 1994). At some wintering areas (e.g. Panama), most first-year birds do not migrate north in the spring, whereas, simultaneously, premigratory adults fatten in preparation for their first northward flight (P. D. O'Hara unpubl. data, Guglielmo 1999). We measured metabolites in sandpipers during (1) winter resi-

dency, when body mass is low and stable, (2) premigration, when adults gain mass at a low rate (0.09 g day^{-1} ; P. D. O'Hara unpubl. data), and (3) migratory stopover, when birds fatten at a high rate ($0.4\text{--}1 \text{ g day}^{-1}$; Butler et al. 1997). We hypothesized that TRIG, an indicator of mass gain, would be higher at migratory stopover than during winter, and in Panama during premigration, TRIG would be higher in adults than yearlings. We expected GLYC and BUTY would follow a pattern opposite to TRIG. We also compared metabolites at two migratory stopover sites.

METHODS

Sample collection.—Wintering (nonmigratory) Western Sandpipers were sampled between 18 December 1995 and 9 February 1996 at Chitré on the Gulf of Panama (8°N , 79°W). Premigratory birds were sampled at Chitré from 4 to 24 March 1996. Adult migrants were sampled during spring northward (30 April–7 May) and "fall" southward migration (16–25 July), 1996 on the mudflats (25,000 ha) at Boundary Bay and Roberts Bank, British Columbia, Canada ($49^{\circ}10'\text{N}$, $123^{\circ}05'\text{W}$). Juveniles were sampled on southward migration in 1996 at Boundary Bay (19–29 August) and at Sidney Island (8–28 August), a small stop-over site located 35 km southwest of Boundary Bay in the southern Strait of Georgia (Lissimore et al. 1999). Due to permit limitations, only females were studied in Panama.

We captured sandpipers with mist nets (Avinet, Dryden, New York) under permits from the Canadian Wildlife Service and INRENARE (Panama). Nets were in constant view, and blood sampling was timed from the moment of capture. In Panama, birds were caught on the falling tide returning from roosting and feeding at inland salt and shrimp ponds. At Boundary Bay and Sidney Island, birds were caught near the end of a high–low–high tide cycle to ensure that they had access to feeding areas for an extended period (6–10 h). About one-half of the samples were taken from the jugular vein of birds collected for body composition analysis (Guglielmo 1999). Approximately 140 birds were sampled from the brachial vein (26 gauge needle, 200–300 μL) with heparinized capillary tubes (VWR Scientific, Buffalo Grove, Illinois) at Chitré, Boundary Bay, and Sidney Island. Whole blood was transferred to heparinized Eppendorf tubes (rinsed with 1,000 IU/mL porcine sodium heparin; SIGMA, USA), and stored above ice in a small cooler. Blood was centrifuged at 6,000 rpm ($2,000 \times g$) for 10 min. Plasma was stored at -20°C until analysis. Animal handling protocols were approved by the Simon Fraser University Animal Care

TABLE 1. Body mass (grams) and plasma lipid metabolite concentrations (mmol L^{-1}) of adult (A) and juvenile (J) Western Sandpipers sampled at a variety of migratory stages and locations (within each sex,

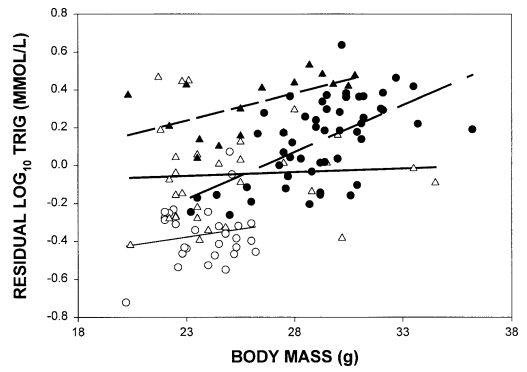


FIG. 1. Plasma triglyceride concentrations of female Western Sandpipers at various sites and seasons plotted against body mass. In nonmigrating

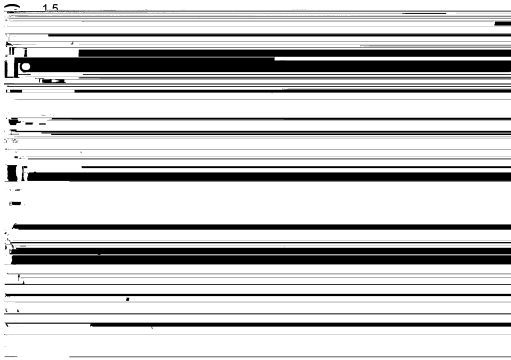


FIG. 2. Residual plasma B-OH-butyrate concentration (controlling for body mass) in wintering and premigrant female Western Sandpipers versus time of day ($R^2 = 0.36$, $P = 0.0008$). Time is minutes from midnight (sunrise approximately 0630 = 390 min; 0900 = 540 min; 1300 = 780 min).

of day interaction ($P = 0.009$). Analysing sites separately, we found no difference in GLYC between spring and fall migrants ($P = 0.91$), or between winter and premigrant birds ($P = 0.70$). Considering only the overlap in sampling times between Sidney Island and Boundary Bay (before 1600) eliminated the site by time of day interaction ($P = 0.49$), and indicated no difference in residual GLYC between the two sites ($P = 0.58$).

B-OH-Butyrate.—BUTY was not significantly related to bleed-time overall ($F = 2.3$, $df = 1$ and 97, $R^2 = 0.01$, $P = 0.14$), or in any stage ($P > 0.35$), but was consistently negatively related to body mass ($\log_{10}\text{BUTY} = -0.036[\text{mass}] + 0.72$; $F = 15.3$, $df = 1$ and 97, $R^2 = 0.14$, $P = 0.0002$). Controlling for body mass, BUTY tended to decline with time of day at all stages, but not significantly ($F = 1.8$, $df = 1$ and 126, $P = 0.18$). However, in Panama, where morning sampling was possible, a decline was readily apparent in the first half of the day (08:00–13:00; $F = 14.5$, $df = 1$ and 26, $R^2 = 0.36$, $P = 0.0008$; Fig. 2). We controlled for body mass and time of day in subsequent analyses.

Sexes were combined because they did not differ ($P = 0.57$) and there was no sex by mass interaction ($P = 0.30$). There was a significant age by mass interaction in fall migrants ($P = 0.01$), but not among Panama samples ($P > 0.53$). Within Panama samples, BUTY did not differ among winter adults, winter juveniles, and premigration season juveniles ($P > 0.18$), however all three had higher BUTY than pre-

migratory adults (evident in Table 1; $P < 0.05$). To compare Panama to Boundary Bay, we analyzed ages separately. BUTY did not differ among winter, premigration season juveniles and fall migrant juveniles ($F = 1.1$, $df = 1$ and 44, $P = 0.34$). In adults, fall data could not be included in the analysis because of a significant stage by mass interaction ($P = 0.04$). However, BUTY in premigrant adults was lower than spring migrant ($P = 0.03$) and winter adults ($P = 0.05$), which did not differ ($P = 0.52$).

DISCUSSION

Bleed-time, body mass and time of day can affect plasma lipid metabolite levels to an extent that could alter the interpretation of field data. Those covariates can be controlled statistically, however, so that hypotheses regarding sex, age, season, or site can be tested. Our most important findings were that (1) whereas in captivity TRIG, BUTY, and GLYC were related to rate of mass change (Williams et al. 1999), only TRIG varied in a predictable manner given the expected patterns of mass change in the field, and (2) TRIG can differ significantly between stopover sites, indicating differences in the rate of mass gain (see also Ydenberg et al. 2002).

Effects of covariates.—Lipid metabolite concentrations were influenced by several variables and interactions (Table 2). TRIG and

TABLE 2. Summary of the effects of several covariates and class variables on plasma lipid metabolite concentrations. (0 = no trend, ? = uncertain, Y = yes, N = no).

Effect	Triglyceride	Glycerol	B-OH-Butyrate
Covariates			
Bleed-time	Negative	Negative	0
Body mass	Positive/0	Negative	Negative
Time of day	0	Negative	Negative/?
Class Variables			
Sex	?	N	N
Sex × mass	Y	N	N
Age	/ = N, ? = Y	N	Y
Age × mass	N	N	Y/N
Stage	Y	N	Y
Stage × mass	Y	Y	Y

plained, respectively, 64 and 21% of the variation in TRIG and BUTY, regardless of whether birds were gaining or losing mass at the time (Williams et al. 1999). TRIG was also positively

during the premigration period, and for TRIG in fall migrant males at Boundary Bay. BUTY was lower in adult birds during premigration, but that can most likely be attributed to the fact that adults were undergoing fattening at that time, rather than to age per se (see below). Juvenile males had higher TRIG than adults at

sults indicate that small, high-quality stopover sites also may be important, especially for individuals with low nutrient stores.

Plasma metabolite analysis offers unique insight into the dynamics of physiological state of wild birds, and should be considered a standard tool for the avian biologist. Future research should be directed at (1) demonstrating in the field that plasma metabolite levels correlate with the rate of mass gain estimated independently (Winker et al. 1992, Gannes 1999, Dunn 2000), and (2) the effects of diet nutrient composition on metabolite to mass change relationships.

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