Fatty Acid Profiles and Relative Mobilization During Fasting in Adipose Tissue Depots of the American Marten (*Martes americana*)

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ABSTRACT: The American marten (*Martes americana*) is a boreal forest marten with low body adiposity but high metabolic rate. The study describes the FA composition in white adipose tissue depots of the species and the influence of food deprivation on them. American marten ($n = 8$) were fasted for 2 d with 7 control animals. Fasting resulted in a 13.4% weight loss, while the relative fat mass was >25% lower in the fasted animals. The FA composition of the fat depots of the trunk was quite similar to other previously studied mustelids with 14:0, 16:0, 18:0, 16:1n-7, 18:1n-9, and 18:2n-6 as the most abundant FA. In the extremities, there were higher proportions of monounsaturated FA (MUFA) and PUFA. Food deprivation decreased the proportions of 16:0 and 16:1n-7, while the proportion of long-chain MUFA increased in the trunk. The mobilization of FA was selective, as 16:1n-7, 18:1n-9, and particular n-3 PUFA were preferentially mobilized. Relative mobilization correlated negatively with the carbon chain length in saturated FA (SFA) and n-9 MUFA. The Δ9-desaturation of SFA enhanced the mobilization of the corresponding MUFA, but the positional isomerism of the first double bond did not correlate consistently with relative mobilization in MUFA or PUFA. In the marten, the FA composition of the extremities was highly resistant to fasting, and the tail tip and the paws contained more long-chain PUFA to prevent the solidification of lipids and to maintain cell membrane fluidity during cooling.

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The American marten (*Martes americana*) is a boreal forest marten, together with the Japanese marten (*M. melampus*), the sable (*M. zibellina*), and the European marten (*M. martes*; 1,2). The American marten occupies a large part of North America (3), inhabiting forests or landscape mosaics with seasonal snow cover (4). The species prefers loose snow with access to subnivean spaces, which has been interpreted as a strategy to minimize energy loss (5). Metabolic costs are a major factor determining the seasonal habitat choice for the American marten. This could be due to the high energetic costs associated with the elongated body shape (6–8). The most important food items in the diet of the American marten are voles, birds, fish, ungulate carcasses, insects, fruits, and berries (9).

The American marten has a low body fat content (approximately 5%) possibly as an adaptation to maintain the lean body shape required for hunting in the burrows of rodents (10). Furthermore, the species does not experience clear seasonal cycles in its body fat content (11). Due to its small gastric ventricle, the American marten has only a limited capacity to consume large amounts of food during a single meal, making fat deposition difficult. The high-protein diet and the high energetic costs of foraging are additional causes for the limited fat storage capacity. However, it has been established that the species can withstand at least 5 d of fasting by entering a state of protein conservation using fat and protein in a ratio of 1.56:1 (12). The plasma concentrations of particular amino acids increase and the excretion of urea decreases in fasted marten probably owing to a high turnover of proteins and urea nitrogen recycling (13). These results indicate that the American marten must be able to mobilize some of its fat reserves effectively for short periods of time. In fact, the periods of naturally occurring fasting are relatively short for the marten, as they are also known to leave their nests daily during the winter with the exception of the harshest weather conditions (14).

In addition to fur, the subcutaneous (sc) fat layer may offer thermal insulation for the marten in the boreal climate. There must also exist a temperature gradient from the skin to the core of the body affecting the FA composition. The challenge of the ambient temperature is even more pronounced on the extremities, such as on the bare food pads and the tip of the tail. Unlike the sc or intra-abdominal (iab) fat depots, the fats of the footpads have to maintain cell membrane fluidity, and it can be hypothesized that they would experience only minor changes in FA composition during food scarcity. For instance, iab fat depots of the semiaquatic American mink (*Mustela vison*) are preferentially mobilized instead of sc fat probably owing to the significance of the sc fat layer as insulation during aquatic predation (15; Nieminen, P., Käkelä, R., Pyykönen, T., and Mustonen, A.-M., unpublished data).

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Abbreviations: BM, body mass; BMI, body mass index; DBI, double bond index; DI, desaturation index; dia, diaphragmatic; iab, intra-abdominal; mes, mesenteric; MUFA, monounsaturated FA; om, omental; rp, retroperitoneal; sc, subcutaneous; SFA, saturated FA; TACL, total average chain length; UFA, unsaturated FA; VLCFA, very long chain FA; WAT, white adipose tissue.

The aim of this study was to describe (i) the FA composition of different white adipose tissue (WAT) depots of the American marten and (ii) the effects of a 48-h fasting period on FA composition. The fasting period of 2 d was considered suitable because, according to previous studies (12), it is significantly shorter than what the species can withstand.

EXPERIMENTAL PROCEDURES

For these experiments 15 American marten (9 males and 6 females) born between 1993 and 2004 were randomly divided into two experimental groups. All the animals were housed singly in standard cages (85 × 30 × 46 cm) with wooden nest boxes (24 × 32 × 35 cm) suspended above ground in an unheated shed at the Canadian Centre for Fur Animal Research, Nova Scotia Agricultural College, in Truro, Nova Scotia, Canada (45.37°N, 63.27°W). Before the experiment the animals were fed for several months with standard fur animal feed (metabolizable energy 1200–1300 kcal kg fresh wt^{-1}; protein minimum 11.0–12.0%, fat 3.0–7.5%, carbohydrates maximum 10.0–11.0%; 16). The marten were provided about 200 g feed or 250 kcal $animal^{-1}$ d^{-1}. They are known to require about 80 kcal d^{-1} when at rest (17). The fasting experiments were conducted January 5–7, 2005. Half of the animals (n = 8) were put on a total 2-d fast, while the other half (n = 7) was fed using the diet and procedure described above. The fed group was fasted overnight before the sampling. Water was available for both experimental groups *ad libitum* during the whole of the study period.

Body masses (BM) were recorded on the first day of the experiment and at sampling, and the body lengths at sampling. Body mass indices (BMI) indicating body adiposity of mustelids (15) were calculated with the formula BMI = BM (kg) × [body $length^3$ (m)]$^{-1}$. The animals were anesthetized with an intramuscular injection of xylazine (Rompun™ 0.17 mL kg^{-1}) and ketamine hydrochloride (Ketalean™ 0.09 mL kg^{-1}). Blood samples were obtained by cardiac punctures using sterile evacuated blood collection tubes with EDTA as an anticoagulant, and the animals were euthanized with an intracardiac injection of pentobarbital (Euthanyl™ 0.44 mL kg^{-1}). The blood was stored on ice until centrifugation at 1000 × g for 15 min at 4°C, after which the plasma was removed. The livers and WAT samples were dissected. The WAT samples collected were as follows: sc interscapular, sc rump, sc ventral, iab omental (om), iab mesenteric (mes), iab diaphragmatic (dia), iab retroperitoneal (rp), intermuscular, tail tip, front paw, and rear paw. The fat samples of the paws were obtained from the tissues situated ventral to the metacarpal and metatarsal bones. At the same time, muscle and kidney samples were obtained for other substudies, and the spleen and pancreas were weighed. All the samples were placed into vials, frozen immediately with liquid nitrogen, and stored at −80°C. The carcasses were also frozen and the different adipose depots dissected and weighed at a later date.

The FA compositions of WAT, plasma, and liver were determined from total lipids. Subsamples of WAT and liver were transmethylated according to Christie (18) by heating with 1% methanolic H_2SO_4 under a nitrogen atmosphere. The same procedure was used for the plasma samples (50 μL); these were first evaporated to near dryness under nitrogen flow and then methylation solvents were added immediately. The FAME that formed were extracted with hexane. The dried and concentrated FAME were analyzed by a gas–liquid chromatograph (GC-FID and GC-MS, 6890N network GC system with autosampler, FID detector, and model 5973 mass selective detector; Agilent Technologies Inc., Palo Alto, CA). The injection volume was 2 μL, and the split ratio 1:20. The injectors were set at 250°C, and the FID and mass interphases were at 250 and 200°C, respectively. Helium was used as a carrier gas (1.8 and 1.0 mL min^{-1} for FID and mass detecting lines, respectively). The obtained peaks were reintegrated manually. The FAME were identified based on retention time, MS, and comparisons with authentic (Sigma, St. Louis, MO) and natural standards of known composition and published reference spectra (http://www.lipidlibrary.co.uk/masspec.html). Quantifications were based on FID responses. The peak areas of the FID chromatograms were converted to mole percentages by using the theoretical response factors (19) and calibrations with quantitative authentic standards. The FA were marked by using the abbreviations: [carbon number]:[number of double bonds] n-[position of the first double bond calculated from the methyl end] (e.g., 22:6n-3). The iso- and anteiso-isomers were abbreviated as *i* and *ai*. If not stated otherwise, PUFA were methylene-interrupted. The FA results are represented as mol%.

The double bond index (DBI) and the total average chain length (TACL), indicating the mean number of double bonds and the mean number of carbon atoms per molecule, respectively, were calculated according to standard formulae (20). The Δ9-desaturation index (Δ9-DI), the ratio of the most important potentially endogenous Δ9-monounsaturated FA (MUFA) to the corresponding saturated FA (SFA), was calculated as [(mol% 14:1n-5) + (mol% 16:1n-7) + (mol% 16:1n-9) + (mol% 18:1n-9) + (mol% 18:1n-7)]/[(mol% 14:0) + (mol% 16:0) + (mol% 18:0)]. The very long chain FA (VLCFA) were calculated as the sum of all FA with a chain length ≥24 carbons (i.e., 24:0 + 24:1n-9; Ref. 21). Relative mobilization was calculated by the formula: [(mol% in the fed animals) – (mol% in the fasted animals)]/(mol% in the fed animals). The FA composition and relative mobilization were also determined for the pooled sc (scapular, rump, and ventral combined) and iab (om, mes, rp and dia combined) fat depots and compared with the results obtained from the extremities.

Multiple comparisons between the experimental groups were performed with one-way ANOVA followed by the Duncan's *post hoc* test. Comparisons between the two experimental groups were performed with the Student's *t*-test for independent samples or, for nonparametric data, with the Mann–Whitney U test. Correlations were calculated using the Spearman correlation coefficient (r_s). A P value less than 0.05 was considered to be statistically significant. The results are presented as mean ± SE.

TABLE 1
Effects of Fasting on the FA (mol%) in Total sc and iab Fats, Fats of the Extremities, and Plasma and Liver of the American Marten[a] (mean ± SE)

	Total sc fat		Total iab fat		Tail tip		Front paws		Rear paws		Plasma		Liver	
FA	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted
12:0	1.40 ± 0.10[b]	1.27 ± 0.09	1.28 ± 0.09[b]	1.18 ± 0.07	0.64 ± 0.07[a]	0.70 ± 0.03	0.85 ± 0.07[a]	1.09 ± 0.08	0.68 ± 0.12[a]	0.88 ± 0.07	0.53 ± 0.15	1.10 ± 0.28	0.10 ± 0.03*	0.76 ± 0.27*
*i*14:0	0.04 ± < 0.01*[a]	0.09 ± 0.02*	0.04 ± < 0.01*[a]	0.08 ± 0.01*	0.12 ± 0.02[b]	0.21 ± 0.10	0.07 ± 0.01[a,b]	0.06 ± < 0.01	0.06 ± 0.01[a,b]	0.06 ± 0.01	0.08 ± 0.01*	0.24 ± 0.05*	0.02 ± < 0.01	0.02 ± < 0.01
14:0	7.86 ± 0.44*[b]	6.77 ± 0.56*	7.17 ± 0.39[b]	6.11 ± 0.42	4.42 ± 0.40[a]	4.92 ± 0.22	4.71 ± 0.28[a]	5.42 ± 0.39	3.93 ± 0.36[a]	4.69 ± 0.29	0.69 ± 0.18*	1.68 ± 0.40*	0.50 ± 0.03*	1.67 ± 0.53*
*i*15:0	0.11 ± 0.01*[b]	0.18 ± 0.03*	0.11 ± 0.01*[b]	0.14 ± 0.01*	0.11 ± 0.01[b]	0.26 ± 0.14	0.08 ± 0.01[a]	0.08 ± < 0.01	0.07 ± 0.01[a]	0.08 ± 0.01	0.16 ± 0.05*	0.31 ± 0.05*	0.02 ± < 0.01*	0.04 ± 0.01*
*ai*15:0	0.06 ± < 0.01*	0.13 ± 0.02*	0.06 ± < 0.01*	0.10 ± 0.01*	0.07 ± 0.01	0.26 ± 0.18	0.07 ± 0.01	0.06 ± < 0.01	0.06 ± 0.01	0.06 ± 0.01	0.04 ± 0.02*	0.13 ± 0.04*	0.02 ± < 0.01	0.03 ± 0.01
15:0	0.31 ± 0.01[b]	0.30 ± 0.03	0.30 ± 0.01*[b]	0.25 ± 0.01*	0.26 ± 0.01[a]	0.28 ± 0.03	0.29 ± 0.02[a,b]	0.24 ± 0.01	0.26 ± 0.01[a]	0.24 ± 0.01	0.23 ± 0.04	0.29 ± 0.05	0.21 ± 0.02	0.18 ± 0.02
*i*16:0	0.06 ± < 0.01*[a]	0.13 ± 0.03*	0.05 ± < 0.01*[a]	0.08 ± 0.01*	0.11 ± 0.02[b]	0.16 ± 0.04	0.08 ± 0.01[a,b]	0.07 ± < 0.01	0.07 ± 0.01[a,b]	0.06 ± 0.01	0.10 ± 0.02	0.18 ± 0.04	0.06 ± 0.01*	0.03 ± < 0.01*
16:0	20.05 ± 0.30*[c]	15.03 ± 0.58*	20.49 ± 0.16*[c]	15.79 ± 0.52*	12.42 ± 0.61[a]	13.17 ± 0.76	15.63 ± 0.67[b]	14.07 ± 0.42	15.41 ± 0.56[b]	14.57 ± 0.31	26.34 ± 3.52	33.01 ± 5.22	24.15 ± 1.28	23.22 ± 1.34
*i*17:0	0.13 ± < 0.01[a]	0.19 ± 0.03	0.13 ± < 0.01[a]	0.14 ± 0.01	0.18 ± 0.02[b]	0.23 ± 0.05	0.14 ± 0.01[a]	0.12 ± 0.01	0.13 ± 0.01[a]	0.12 ± 0.01	0.32 ± 0.06	0.31 ± 0.05	0.28 ± 0.02*	0.17 ± 0.03*
*ai*17:0	0.14 ± < 0.01*[a]	0.25 ± 0.04*	0.14 ± < 0.01*[a]	0.19 ± 0.02*	0.19 ± 0.01[b]	0.23 ± 0.04	0.18 ± 0.01[b]	0.18 ± 0.01	0.17 ± 0.02[a,b]	0.17 ± 0.01	0.11 ± 0.03	0.20 ± 0.04	0.12 ± 0.02	0.15 ± 0.02
17:0	0.39 ± 0.01[c]	0.43 ± 0.04	0.41 ± 0.01[c]	0.43 ± 0.02	0.25 ± 0.02[a]	0.26 ± 0.02	0.33 ± 0.02[b]	0.29 ± 0.02	0.32 ± 0.02[b]	0.27 ± 0.01	0.77 ± 0.11	0.82 ± 0.12	0.91 ± 0.06*	0.65 ± 0.07*
*i*18:0	0.08 ± < 0.01[a]	0.13 ± 0.02	0.07 ± < 0.01[a]	0.12 ± 0.02	0.11 ± 0.01[b]	0.16 ± 0.03	0.08 ± 0.01[a]	0.08 ± 0.01	0.06 ± 0.01[a]	0.09 ± 0.02	0.11 ± 0.04	0.17 ± 0.03	0.06 ± < 0.01*	0.04 ± < 0.01*
18:0	5.72 ± 0.15*[a]	7.58 ± 0.41*	6.63 ± 0.15*[b]	9.14 ± 0.62*	5.26 ± 0.62[a,b]	5.49 ± 0.61	5.60 ± 0.58[a,b]	6.49 ± 1.01	6.22 ± 0.68[a,b]	6.25 ± 0.70	21.38 ± 2.82	20.04 ± 2.94	23.84 ± 0.75	18.45 ± 2.48
19:0	0.09 ± < 0.01*	0.23 ± 0.04*	0.10 ± < 0.01*	0.19 ± 0.02*	0.10 ± 0.01	0.12 ± 0.02	0.08 ± 0.01	0.10 ± 0.01	0.09 ± 0.01	0.09 ± 0.01	0.19 ± 0.04*	0.35 ± 0.07*	0.16 ± 0.02	0.15 ± 0.02
20:0	0.18 ± 0.01*	0.41 ± 0.04*	0.19 ± 0.01*	0.38 ± 0.03*	0.21 ± 0.04	0.26 ± 0.06	0.17 ± 0.04	0.15 ± 0.03	0.17 ± 0.03	0.16 ± 0.02	0.20 ± 0.04*	0.49 ± 0.07*	0.07 ± < 0.01	0.08 ± 0.01
22:0	0.04 ± < 0.01*[a]	0.21 ± 0.05*	0.05 ± 0.01*[a]	0.22 ± 0.04*	0.25 ± 0.06[b]	0.24 ± 0.04	0.16 ± 0.04[b]	0.15 ± 0.03	0.17 ± 0.03[b]	0.17 ± 0.02	0.37 ± 0.06*	0.71 ± 0.12*	0.10 ± 0.01	0.08 ± 0.01
24:0	0.03 ± < 0.01*[a]	0.37 ± 0.12*	0.02 ± < 0.01*[a]	0.19 ± 0.05*	0.47 ± 0.10[b]	0.48 ± 0.08	0.28 ± 0.09[b]	0.27 ± 0.05	0.31 ± 0.06[b]	0.33 ± 0.04	0.10 ± 0.02*	0.60 ± 0.19*	0.08 ± 0.01	0.10 ± 0.01
Σ:0	36.68 ± 0.93*[c]	33.71 ± 0.50*	37.23 ± 0.62*[c]	34.73 ± 0.58*	25.16 ± 1.60 [a]	27.43 ± 2.01	28.78 ± 1.58[b]	28.92 ± 1.10	28.18 ± 1.20[a,b]	28.28 ± 0.83	51.71 ± 6.92	60.64 ± 8.81	50.69 ± 0.88*	45.83 ± 1.57*
14:1n-9	0.025 ± 0.002*[a]	0.111 ± 0.038*	0.022 ± 0.002*[a]	0.066 ± 0.014*	0.050 ± 0.007[b]	0.049 ± 0.010	0.040 ± 0.012[a,b]	0.030 ± 0.004	0.026 ± 0.006[a]	0.027 ± 0.004	0.080 ± 0.044	0.117 ± 0.031	0.012 ± 0.003*	0.045 ± 0.015*
14:1n-7	0.064 ± 0.002*[a]	0.169 ± 0.036*	0.059 ± 0.002*[a]	0.112 ± 0.010*	0.107 ± 0.008 [c]	0.106 ± 0.007	0.085 ± 0.010[b]	0.091 ± 0.008	0.066 ± 0.007[a,b]	0.073 ± 0.005	0.026 ± 0.004*	0.091 ± 0.023*	0.051 ± 0.013	0.073 ± 0.018
14:1n-5	0.211 ± 0.015*[b]	0.344 ± 0.039*	0.139 ± 0.007*[a]	0.229 ± 0.020*	1.634 ± 0.190[d]	1.734 ± 0.205	0.693 ± 0.075*[c]	1.046 ± 0.137*	0.642 ± 0.065*[c]	0.845 ± 0.043*	0.049 ± 0.012*	0.102 ± 0.014*	0.016 ± 0.004	0.071 ± 0.027
15:1n-8	0.027 ± 0.001*[a]	0.135 ± 0.042*	0.026 ± 0.001*[a]	0.077 ± 0.013*	0.106 ± 0.018[b]	0.196 ± 0.058	0.083 ± 0.018[b]	0.086 ± 0.010	0.075 ± 0.014[b]	0.113 ± 0.046	0.263 ± 0.117	0.319 ± 0.066	0.090 ± 0.024	0.053 ± 0.015
15:1n-6	0.013 ± 0.001*[b]	0.103 ± 0.040*	0.009 ± 0.001*[a]	0.051 ± 0.013*	0.060 ± 0.004[d]	0.067 ± 0.006	0.037 ± 0.006[c]	0.040 ± 0.004	0.028 ± 0.003[c]	0.032 ± 0.003	0.021 ± 0.007*	0.110 ± 0.022*	0.018 ± 0.004	0.017 ± 0.005
16:1n-9	0.520 ± 0.011*[b]	0.589 ± 0.016*	0.511 ± 0.009*[b]	0.558 ± 0.019*	0.502 ± 0.035[b]	0.443 ± 0.012	0.518 ± 0.027[b]	0.481 ± 0.017	0.442 ± 0.017[a]	0.429 ± 0.015	0.166 ± 0.025	0.164 ± 0.013	0.238 ± 0.047	0.334 ± 0.081
16:1n-7	4.468 ± 0.235*[b]	2.476 ± 0.197*	3.600 ± 0.109*[a]	1.989 ± 0.151*	11.130 ± 0.783[d]	11.000 ± 1.134	7.900 ± 0.838[c]	7.486 ± 1.086	7.960 ± 0.553[c]	7.734 ± 0.794	0.573 ± 0.089	0.428 ± 0.091	0.973 ± 0.171	1.280 ± 0.344
16:1n-5	0.087 ± 0.003*[a]	0.180 ± 0.043*	0.082 ± 0.003*[a]	0.124 ± 0.018*	0.184 ± 0.014[c]	0.220 ± 0.020	0.154 ± 0.015[b,c]	0.151 ± 0.013	0.142 ± 0.009[b]	0.138 ± 0.008	0.089 ± 0.013	0.108 ± 0.015	0.318 ± 0.077	0.304 ± 0.114
17:1-br	0.164 ± 0.008*[b]	0.355 ± 0.040*	0.165 ± 0.008*[b]	0.351 ± 0.033*	0.136 ± 0.013[a,b]	0.137 ± 0.007	0.135 ± 0.011[a,b]	0.154 ± 0.017	0.112 ± 0.009[a]	0.124 ± 0.011	0.203 ± 0.040	0.284 ± 0.025	0.408 ± 0.095	0.308 ± 0.070
17:1n-8	0.192 ± 0.010[a]	0.204 ± 0.031	0.165 ± 0.006[a]	0.149 ± 0.009	0.384 ± 0.018[c]	0.362 ± 0.025	0.346 ± 0.025[b,c]	0.282 ± 0.024	0.342 ± 0.014[b]	0.315 ± 0.018	0.104 ± 0.023	0.179 ± 0.038	0.099 ± 0.016	0.071 ± 0.016
18:1n-9	28.85 ± 0.90	26.55 ± 1.37	28.61 ± 0.74*	26.03 ± 0.98*	29.23 ± 1.64	27.10 ± 1.77	30.09 ± 1.51	28.25 ± 1.27	30.44 ± 1.59	29.29 ± 1.25	4.13 ± 0.88	3.73 ± 1.24	5.72 ± 0.89	8.24 ± 1.72
18:1n-7	2.528 ± 0.071[a]	2.399 ± 0.032	2.536 ± 0.055[a]	2.445 ± 0.043	3.412 ± 0.164[b]	3.154 ± 0.086	3.345 ± 0.120[b]	3.118 ± 0.071	3.520 ± 0.145[b]	3.236 ± 0.091	1.063 ± 0.225	1.190 ± 0.363	1.966 ± 0.107	2.220 ± 0.075
18:1n-5	0.132 ± 0.004	0.196 ± 0.031	0.131 ± 0.004	0.132 ± 0.006	0.154 ± 0.016	0.149 ± 0.008	0.154 ± 0.020	0.119 ± 0.007	0.139 ± 0.012	0.133 ± 0.010	0.061 ± 0.010*	0.151 ± 0.047*	0.088 ± 0.018	0.079 ± 0.011
19:1n-10	0.136 ± 0.003*[a]	0.226 ± 0.029*	0.129 ± 0.003*[a]	0.168 ± 0.007*	0.154 ± 0.006[b]	0.155 ± 0.009	0.132 ± 0.004[a]	0.134 ± 0.005	0.130 ± 0.006[a]	0.132 ± 0.007	0.045 ± 0.008*	0.113 ± 0.024*	0.075 ± 0.013	0.069 ± 0.013
19:1n-8	0.066 ± 0.002*	0.179 ± 0.041*	0.064 ± 0.001*	0.105 ± 0.009*	0.084 ± 0.014	0.095 ± 0.012	0.081 ± 0.008	0.070 ± 0.002	0.078 ± 0.012	0.069 ± 0.003	0.036 ± 0.006*	0.138 ± 0.022*	0.025 ± 0.004	0.037 ± 0.005
20:1n-11	1.126 ± 0.047*[b]	2.023 ± 0.138*	1.240 ± 0.047*[b]	2.223 ± 0.141*	0.640 ± 0.064[a]	0.692 ± 0.080	0.767 ± 0.096[a]	0.974 ± 0.090	0.925 ± 0.232[a,b]	0.959 ± 0.099	0.074 ± 0.004*	0.170 ± 0.033*	0.099 ± 0.014*	0.203 ± 0.034*
20:1n-9	2.493 ± 0.095*[b]	3.618 ± 0.212*	2.739 ± 0.135*[b]	3.580 ± 0.167*	0.997 ± 0.082[a]	1.047 ± 0.139	1.173 ± 0.113[a]	1.358 ± 0.093	1.264 ± 0.231[a]	1.328 ± 0.125	0.186 ± 0.037	0.265 ± 0.081	0.355 ± 0.033	0.475 ± 0.056
20:1n-7	0.141 ± 0.005*[b]	0.250 ± 0.016*	0.149 ± 0.004*[b]	0.209 ± 0.011*	0.082 ± 0.009[a]	0.096 ± 0.011	0.080 ± 0.012[a]	0.091 ± 0.008	0.079 ± 0.007[a]	0.079 ± 0.005	0.061 ± 0.009	0.074 ± 0.011	0.058 ± 0.009	0.050 ± 0.006
20:1n-5	0.026 ± 0.002*	0.091 ± 0.021*	0.026 ± 0.002*	0.047 ± 0.005*	0.025 ± 0.007	0.023 ± 0.004	0.018 ± 0.002	0.018 ± 0.002	0.015 ± 0.004	0.015 ± 0.002	0.040 ± 0.012	0.070 ± 0.014	0.004 ± 0.001	0.005 ± 0.001
22:1n-11	1.118 ± 0.065*[b]	1.766 ± 0.114*	1.340 ± 0.071*[c]	1.821 ± 0.113*	0.307 ± 0.042[a]	0.322 ± 0.037	0.290 ± 0.041[a]	0.309 ± 0.049	0.267 ± 0.032[a]	0.282 ± 0.029	0.197 ± 0.015	0.176 ± 0.039	0.172 ± 0.014	0.152 ± 0.019
22:1n-9	0.167 ± 0.008*[b]	0.389 ± 0.047*	0.179 ± 0.008*[b]	0.321 ± 0.024*	0.174 ± 0.026[b]	0.216 ± 0.040	0.113 ± 0.021[a]	0.122 ± 0.023	0.103 ± 0.018[a]	0.121 ± 0.015	0.065 ± 0.017	0.101 ± 0.013	0.048 ± 0.009	0.045 ± 0.007
22:1n-7	0.030 ± 0.002*[a]	0.120 ± 0.030*	0.027 ± 0.002*[a]	0.065 ± 0.010*	0.067 ± 0.013[c]	0.107 ± 0.022	0.051 ± 0.017[b,c]	0.041 ± 0.005	0.036 ± 0.009[a,b]	0.031 ± 0.003	0.068 ± 0.025	0.128 ± 0.022	0.012 ± 0.003	0.012 ± 0.004
24:1n-9	0.084 ± 0.006*[a]	0.543 ± 0.138*	0.088 ± 0.011*[a]	0.480 ± 0.096*	0.711 ± 0.127[b]	0.689 ± 0.110	0.507 ± 0.141[b]	0.460 ± 0.091	0.480 ± 0.089[b]	0.450 ± 0.052	0.349 ± 0.110	0.924 ± 0.249	0.128 ± 0.021	0.192 ± 0.026
Σ:1	42.67 ± 1.24[a,b]	43.01 ± 1.16	42.04 ± 1.02[a]	41.33 ± 0.99	50.33 ± 1.86[c]	48.16 ± 2.75	46.80 ± 2.18[a,b,c]	44.90 ± 2.13	47.31 ± 2.16[b,c]	45.95 ± 1.99	7.95 ± 1.16	9.13 ± 1.76	10.97 ± 1.48	14.33 ± 2.28
Δ9-DI	1.12 ± 0.07[a]	1.10 ± 0.04	1.05 ± 0.04[a]	1.02 ± 0.04	2.16 ± 0.23[b]	1.93 ± 0.22	1.70 ± 0.19[b]	1.59 ± 0.15	1.72 ± 0.14[b]	1.65 ± 0.13	0.16 ± 0.04	0.16 ± 0.05	0.18 ± 0.03	0.30 ± 0.07
16:2n-4	0.155 ± 0.007	0.146 ± 0.024	0.143 ± 0.007*	0.104 ± 0.008*	0.152 ± 0.005	0.141 ± 0.008	0.133 ± 0.012	0.120 ± 0.014	0.122 ± 0.010	0.111 ± 0.009	0.061 ± 0.006*	0.196 ± 0.043*	0.046 ± 0.010	0.064 ± 0.018
18:2n-7	0.100 ± 0.008[a]	0.168 ± 0.033	0.089 ± 0.004[a]	0.099 ± 0.008	0.143 ± 0.013[b]	0.151 ± 0.006	0.131 ± 0.013[b]	0.110 ± 0.011	0.128 ± 0.016[b]	0.123 ± 0.010	0.051 ± 0.008*	0.085 ± 0.013*	0.094 ± 0.012	0.075 ± 0.022
18:2n-6	13.52 ± 0.17	13.23 ± 0.30	13.67 ± 0.18	13.83 ± 0.23	12.64 ± 0.64	11.80 ± 0.25	13.79 ± 0.44	13.69 ± 0.26	13.42 ± 0.19	13.77 ± 0.26	16.03 ± 3.78	6.99 ± 2.38	9.93 ± 0.41	11.53 ± 0.81
18:2n-4	0.111 ± 0.003[b]	0.159 ± 0.026	0.099 ± 0.004*[a]	0.119 ± 0.008*	0.141 ± 0.023[a,b]	0.125 ± 0.008	0.113 ± 0.005[a,b]	0.109 ± 0.005	0.109 ± 0.003[a,b]	0.108 ± 0.005	0.074 ± 0.013*	0.184 ± 0.060*	0.080 ± 0.006	0.070 ± 0.008
*c,t*18:2	0.060 ± 0.005[b]	0.149 ± 0.049	0.047 ± 0.002*[a]	0.071 ± 0.008*	0.143 ± 0.014[c]	0.234 ± 0.093	0.110 ± 0.019[c]	0.095 ± 0.010	0.110 ± 0.010[c]	0.103 ± 0.007	0.040 ± 0.008*	0.182 ± 0.040*	0.014 ± 0.004	0.023 ± 0.004
20:2n-6	0.168 ± 0.003*[a]	0.254 ± 0.015*	0.171 ± 0.004*[a]	0.248 ± 0.012*	0.214 ± 0.008[b]	0.337 ± 0.140	0.211 ± 0.016[b]	0.223 ± 0.016	0.225 ± 0.012[b]	0.218 ± 0.010	0.214 ± 0.056	0.286 ± 0.058	0.151 ± 0.005	0.174 ± 0.016
Σ:2	14.12 ± 0.16	14.11 ± 0.21	14.22 ± 0.18	14.47 ± 0.22	13.43 ± 0.61	12.79 ± 0.25	14.48 ± 0.43	14.35 ± 0.26	14.12 ± 0.19	14.43 ± 0.26	16.47 ± 3.73*	7.93 ± 2.28*	10.31 ± 0.39	11.94 ± 0.81
18:3n-6	0.137 ± 0.005[c]	0.155 ± 0.028	0.125 ± 0.004*[c]	0.102 ± 0.005*	0.103 ± 0.006[b]	0.102 ± 0.008	0.104 ± 0.005[b]	0.085 ± 0.007	0.081 ± 0.004[a]	0.077 ± 0.003	0.282 ± 0.080	0.227 ± 0.032	0.227 ± 0.035	0.219 ± 0.050
18:3n-3	0.911 ± 0.025*[b]	0.587 ± 0.026*	0.894 ± 0.027*[b]	0.544 ± 0.031*	0.751 ± 0.045[a]	0.657 ± 0.040	0.761 ± 0.045[a]	0.654 ± 0.068	0.734 ± 0.027[a]	0.667 ± 0.049	0.312 ± 0.083	0.217 ± 0.035	0.286 ± 0.011	0.377 ± 0.099
20:3n-6	0.175 ± 0.006*[a]	0.328 ± 0.043*	0.183 ± 0.010*[a]	0.356 ± 0.038*	0.412 ± 0.039[b]	0.453 ± 0.052	0.360 ± 0.032[b]	0.392 ± 0.047	0.380 ± 0.054[b]	0.414 ± 0.052	0.553 ± 0.142	0.480 ± 0.161	0.901 ± 0.061*	0.502 ± 0.052*
20:3n-3	0.040 ± 0.002*[a]	0.133 ± 0.043*	0.038 ± 0.002*[a]	0.064 ± 0.008*	0.125 ± 0.015[c]	0.157 ± 0.031	0.071 ± 0.007[b]	0.075 ± 0.008	0.063 ± 0.009[b]	0.052 ± 0.003	0.055 ± 0.012*	0.116 ± 0.014*	0.038 ± 0.005	0.041 ± 0.003

(continued)

TABLE 1 (continued)

FA	Total sc fat		Total iab fat		Tail tip		Front paws		Rear paws		Plasma		Liver	
	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted
Σ:3	1.263 ± 0.032	1.203 ± 0.118	1.240 ± 0.037*	1.066 ± 0.042*	1.391 ± 0.043	1.369 ± 0.065	1.296 ± 0.027	1.205 ± 0.039	1.258 ± 0.053	1.210 ± 0.042	1.202 ± 0.283	1.041 ± 0.196	1.453 ± 0.084*	1.139 ± 0.110*
18:4n-3	0.287 ± 0.015^{b}	0.246 ± 0.035	0.278 ± 0.014^{ab}	0.187 ± 0.015*	0.216 ± 0.018^{a}	0.193 ± 0.012	0.186 ± 0.017^{a}	0.161 ± 0.018	0.172 ± 0.018^{a}	0.145 ± 0.010	0.126 ± 0.013*	0.199 ± 0.027*	0.050 ± 0.009	0.113 ± 0.038
18:4n-1	0.049 ± 0.003^{a}	0.081 ± 0.028	0.041 ± 0.002^{a}	0.042 ± 0.008	0.090 ± 0.004^{c}	0.087 ± 0.008	0.068 ± 0.002^{b}	0.057 ± 0.007	0.064 ± 0.007^{b}	0.056 ± 0.006	0.046 ± 0.014*	0.122 ± 0.030*	0.031 ± 0.006	0.036 ± 0.009
20:4n-6	0.445 ± 0.022*^{a}	1.415 ± 0.349*	0.516 ± 0.101*^{a}	2.209 ± 0.438*	2.476 ± 0.261^{b}	2.907 ± 0.457	2.184 ± 0.258^{b}	2.827 ± 0.470	2.436 ± 0.446^{b}	2.803 ± 0.463	6.859 ± 1.837	6.038 ± 2.163	7.768 ± 0.676	6.692 ± 0.847
20:4n-3	0.143 ± 0.006^{a,b}	0.245 ± 0.064	0.139 ± 0.006^{a}	0.155 ± 0.011	0.195 ± 0.006^{c}	0.200 ± 0.016	0.167 ± 0.011^{b}	0.145 ± 0.003	0.152 ± 0.007^{a,b}	0.142 ± 0.007	0.156 ± 0.023	0.282 ± 0.062	0.112 ± 0.009	0.121 ± 0.019
22:4n-6	0.172 ± 0.009*^{a}	0.489 ± 0.073*	0.189 ± 0.017*^{a}	0.513 ± 0.060*	0.331 ± 0.035^{b}	0.380 ± 0.063	0.320 ± 0.051^{b}	0.371 ± 0.059	0.293 ± 0.047^{b}	0.352 ± 0.044	0.160 ± 0.030	0.499 ± 0.160	0.246 ± 0.041	0.251 ± 0.026
22:4n-3	0.033 ± 0.002*^{a}	0.155 ± 0.045*	0.028 ± 0.002*^{a}	0.072 ± 0.014*	0.101 ± 0.023^{b}	0.103 ± 0.032	0.062 ± 0.018^{a,b}	0.055 ± 0.008	0.036 ± 0.007^{a,b}	0.041 ± 0.008	2.001 ± 0.941	0.580 ± 0.368	0.047 ± 0.012	0.045 ± 0.010
Σ:4	1.128 ± 0.052*^{a}	2.631 ± 0.564*	1.190 ± 0.125*^{a}	3.178 ± 0.517*	3.408 ± 0.337^{b}	3.868 ± 0.531	2.987 ± 0.311^{b}	3.616 ± 0.515	3.152 ± 0.498^{b}	3.538 ± 0.511	9.347 ± 0.917	7.720 ± 2.200	8.254 ± 0.671	7.258 ± 0.799
20:5n-3	0.646 ± 0.046^{a}	0.765 ± 0.197	0.629 ± 0.067^{a}	0.807 ± 0.135	1.901 ± 0.152^{b}	1.791 ± 0.147	1.672 ± 0.164^{b}	1.696 ± 0.206	1.801 ± 0.266^{b}	1.723 ± 0.217	5.559 ± 1.699	2.132 ± 0.742	5.424 ± 0.301*	3.578 ± 0.276*
21:5n-3	0.096 ± 0.006^{ab}	0.192 ± 0.038*	0.091 ± 0.006^{b}	0.114 ± 0.010	0.133 ± 0.029^{ab}	0.143 ± 0.031	0.085 ± 0.010^{a,b}	0.081 ± 0.003	0.063 ± 0.011^{a}	0.059 ± 0.004	0.147 ± 0.088	0.123 ± 0.026	0.026 ± 0.003	0.049 ± 0.016
22:5n-6	0.164 ± 0.011*	0.477 ± 0.109*	0.160 ± 0.011*	0.310 ± 0.027*	0.166 ± 0.020	0.183 ± 0.024	0.147 ± 0.016	0.212 ± 0.022	0.142 ± 0.023	0.169 ± 0.016	3.933 ± 1.792	3.092 ± 1.664	0.246 ± 0.030*	0.366 ± 0.036*
22:5n-3	0.695 ± 0.028*^{a}	1.132 ± 0.118*	0.703 ± 0.032*^{a}	1.129 ± 0.077*	0.978 ± 0.054^{b}	1.097 ± 0.086	0.959 ± 0.066^{b}	1.092 ± 0.083	0.963 ± 0.076^{a,b}	1.035 ± 0.082	0.591 ± 0.182	1.125 ± 0.423	1.371 ± 0.069	1.372 ± 0.061
Σ:5	1.601 ± 0.084*^{a}	2.567 ± 0.448*	1.583 ± 0.107*^{a}	2.359 ± 0.233*	3.177 ± 0.247^{b}	3.215 ± 0.258	2.863 ± 0.225^{b}	3.080 ± 0.285	2.969 ± 0.363^{b}	2.985 ± 0.310	10.231 ± 0.536*	6.472 ± 1.350*	7.067 ± 0.377*	5.365 ± 0.295*
22:6n-3	2.541 ± 0.159	2.772 ± 0.183	2.501 ± 0.151	2.868 ± 0.135	3.112 ± 0.280	3.173 ± 0.240	2.792 ± 0.304	3.933 ± 0.345	3.013 ± 0.329	3.600 ± 0.414	3.094 ± 1.059	7.068 ± 2.365	11.262 ± 0.658	14.145 ± 1.167
ΣPUFA	20.65 ± 0.42*^{a}	23.28 ± 1.20*	20.73 ± 0.50*^{a}	23.95 ± 0.90*	24.52 ± 0.51^{b}	24.41 ± 0.89	24.42 ± 0.82^{b}	26.18 ± 1.10	24.51 ± 1.20^{b}	25.76 ± 1.25	40.34 ± 5.83	30.23 ± 7.11	38.35 ± 1.84	39.85 ± 1.45
Σ:n-6	14.79 ± 0.20*^{a}	16.35 ± 0.41*	15.01 ± 0.26*^{a}	17.57 ± 0.56*	16.34 ± 0.47^{b}	16.16 ± 0.52	17.11 ± 0.48^{b}	17.80 ± 0.59	16.98 ± 0.58^{b}	17.80 ± 0.66	28.03 ± 4.01	17.62 ± 4.01	19.46 ± 1.02	19.74 ± 0.72
Σ:n-3	5.39 ± 0.27^{a}	6.23 ± 0.69	5.30 ± 0.28^{a}	5.94 ± 0.36	7.51 ± 0.51^{b}	7.51 ± 0.45	6.75 ± 0.47^{b}	7.89 ± 0.57	7.00 ± 0.68^{b}	7.46 ± 0.64	12.04 ± 2.04	11.84 ± 3.39	18.62 ± 0.98	19.84 ± 1.01
n–3/n-6	0.36 ± 0.02^{a}	0.37 ± 0.03	0.35 ± 0.02^{a}	0.33 ± 0.01	0.46 ± 0.04^{b}	0.46 ± 0.02	0.39 ± 0.02^{a,b}	0.44 ± 0.02	0.41 ± 0.03^{a,b}	0.41 ± 0.02	0.42 ± 0.03	0.65 ± 0.15	0.96 ± 0.04	1.01 ± 0.04
ΣVLCFA	0.111 ± 0.009*^{a}	0.916 ± 0.254*	0.113 ± 0.015*^{a}	0.672 ± 0.141*	1.180 ± 0.231^{b}	1.169 ± 0.190	0.784 ± 0.227^{b}	0.734 ± 0.141	0.795 ± 0.151^{b}	0.775 ± 0.088	0.445 ± 0.124*	1.528 ± 0.170*	0.213 ± 0.025	0.287 ± 0.035
UFA/SFA	1.76 ± 0.08*^{a}	1.98 ± 0.04*	1.71 ± 0.05*^{a}	1.91 ± 0.06*	3.08 ± 0.29^{b}	2.77 ± 0.25	2.54 ± 0.21^{b}	2.49 ± 0.13	2.59 ± 0.16^{b}	2.56 ± 0.11	1.15 ± 0.26	0.93 ± 0.28	0.98 ± 0.03*	1.20 ± 0.09*
DBI	0.51 ± 0.01^{a}	0.52 ± 0.01	0.51 ± 0.01^{a}	0.51 ± 0.01	0.60 ± 0.02^{b}	0.57 ± 0.03	0.56 ± 0.02^{b}	0.55 ± 0.02	0.57 ± 0.02^{b}	0.56 ± 0.02	0.21 ± 0.03	0.18 ± 0.04	0.22 ± 0.01	0.26 ± 0.02
TACL	17.29 ± 0.03*^{a}	17.54 ± 0.04*	17.37 ± 0.02*^{a,b}	17.62 ± 0.04*	17.28 ± 0.07^{a}	17.21 ± 0.06	17.39 ± 0.03^{a,b}	17.39 ± 0.09	17.48 ± 0.04^{b}	17.44 ± 0.06	17.98 ± 0.12	17.74 ± 0.25	18.20 ± 0.07	18.18 ± 0.13

[a]An asterisk (*) indicates a significant difference between the fed and fasted animals (*t*-test, Mann–Whitney U test, $P < 0.05$); dissimilar superscripts indicate that the values of subcutaneous (sc), intra-abdominal (iab), and extremity fats of the fed group differ at $P < 0.05$ (one-way ANOVA). Δ9-DI = Δ9-desaturation index, VLCFA = very long chain FA (chain length ≥ 24 C), UFA = unsaturated FA, SFA = saturated FA, DBI = double bond index, TACL = total average chain length.

RESULTS

The average initial (fed: 884 ± 70 g, fasted: 849 ± 63 g) or final (fasted: 734 ± 56 g) BM of the marten did not differ between the experimental groups. The fasted marten lost approximately 113 g or 13.4% of BM during the 2-d fasting period. The absolute or relative masses of the different fat depots did not differ between the experimental groups (sc interscapular: fed 0.27 ± 0.05 vs. fasted 0.15 ± 0.04 g; sc rump: 0.16 ± 0.05 vs. 0.15 ± 0.05 g; sc ventral: 1.29 ± 0.57 vs. 0.61 ± 0.16 g; iab om: 4.94 ± 1.66 vs. 1.93 ± 0.61 g; iab mes: 2.44 ± 0.78 vs. 1.19 ± 0.24 g; iab dia: 0.68 ± 0.27 vs. 0.33 ± 0.11 g; iab rp: 5.58 ± 2.18 vs. 3.29 ± 1.79 g; intermuscular: 8.03 ± 0.85 vs. 7.52 ± 0.57 g; total fat percentage: 2.74 ± 0.56 vs. 2.06 ± 0.24%, $P > 0.05$). The total fat mass (23.4 ± 4.4 vs. 15.2 ± 2.2 g) was lower in the fasted animals ($P < 0.05$). The calculated BMI correlated strongly with the total fat mass ($rs = 0.604$, $P < 0.05$) and the fat percentage ($rs = 0.804$, $P < 0.01$). The initial BMI did not differ between the experimental groups, but the BMI was significantly lower in the fasted animals at the end of the study (12.9 ± 0.7 vs. 10.6 ± 0.2 kg $(m^3)^{-1}$; $P < 0.05$). Many of the marten in the fasted group were physically active and exhibited stereotypical behavior and signs of stress, such as hair biting.

The most abundant FA (≥1 mol%) in the sc and iab fat depots of the marten were 12:0, 14:0, 16:0, 18:0, 16:1n-7, 18:1n-9, 18:1n-7, 20:1n-11, 20:1n-9, 22:1n-11, 18:2n-6, and 22:6n-3 (Table 1). In the extremities the pattern was mostly the same, but the proportions of 12:0, 20:1n-11, and 20:1n-9 were clearly lower, whereas the proportions of 14:1n-5, 20:4n-6, and 20:5n-3 were higher than in the trunk fat. Generally, the extremities had higher proportions of unsaturated FA (UFA) than the iab or sc depots. In fact, the DBI, Δ9-DI, total PUFA, and the sums of 4n- and 5n-PUFA were all higher in the extremities. In the plasma and livers the proportions of SFA and particular PUFA were higher than in any of the fat depots; in particular, the proportions of 16:0 and 18:0 were two to three times higher than in the WAT, and also the proportions of 20:4n-6 and 20:5n-3 were elevated. On the other hand, the proportions of certain monoenes, especially 18:1n-9 and 18:1n-7, were fairly low in the plasma and livers.

Food deprivation caused numerous differences in the proportions of FA in the fat depots (Tables 1–3). The sum of SFA decreased in the sc scapular and iab rp depots and in the pooled trunk fats, mostly owing to significant decreases in the proportion of 16:0, whereas the proportions of 18:0, 19:0, 20:0, 22:0, and 24:0 mostly increased in the fasted animals. Also the proportions of most MUFA were higher in the fasted group in most fat depots with the exception of 16:1n-7, the proportions of which decreased in all sc and iab tissues. In the PUFA the proportions of 20:2n-6, 20:3n-6, 22:4n-6, 22:4n-3, 22:5n-6, and 22:5n-3 increased, whereas the proportions of 18:3n-3 and 18:4n-3 were lower in the fasted marten. In the pooled trunk fats, the proportions of 4n- and 5n-PUFA increased due to fasting. In a similar manner, the proportions of n-6 PUFA and VLCFA as well as the TACL were higher in the fasted group in the pooled sc and iab fats. In the extremities, the effects of fasting were minor. In plasma, the proportions of several SFA,

TABLE 2
Effects of Fasting on the Composition of Saturated and Monounsaturated FA (mol%) in Adipose Tissues of the American Marten[a] (mean ± SE)

	Scapular sc fat		Rump sc fat		Ventral sc fat		Mesenteric fat		Omental fat		Retroperitoneal fat		Diaphragmatic fat	
FA	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted
12:0	1.50 ± 0.15	1.22 ± 0.15	1.26 ± 0.22	1.28 ± 0.13	1.39 ± 0.17	1.31 ± 0.18	1.38 ± 0.18	1.17 ± 0.15	1.35 ± 0.17	1.29 ± 0.12	1.19 ± 0.16	1.05 ± 0.13	1.15 ± 0.29	1.21 ± 0.16
14:0	8.18 ± 0.67	6.56 ± 1.06	7.28 ± 0.96	6.90 ± 0.90	7.95 ± 0.77	6.84 ± 1.05	7.50 ± 0.84	5.95 ± 0.83	7.01 ± 0.67	6.42 ± 0.79	7.22 ± 0.74	5.69 ± 0.95	6.80 ± 1.22	6.39 ± 0.93
15:0	0.31 ± 0.01	0.27 ± 0.02	0.30 ± 0.02	0.27 ± 0.02	0.30 ± 0.01	0.34 ± 0.09	0.31 ± 0.01	0.28 ± 0.02	0.31 ± 0.01*	0.26 ± 0.02*	0.29 ± 0.01*	0.23 ± 0.02*	0.29 ± 0.02*	0.24 ± 0.01*
16:0	20.48 ± 0.47*	15.12 ± 1.15*	19.50 ± 0.56*	14.66 ± 1.00*	20.02 ± 0.53*	15.31 ± 0.95*	20.87 ± 0.32*	17.20 ± 0.84*	20.59 ± 0.30*	17.16 ± 1.12*	20.17 ± 0.31*	14.04 ± 0.87*	20.19 ± 0.28*	14.74 ± 0.99*
17:0	0.39 ± 0.02	0.44 ± 0.06	0.38 ± 0.02	0.42 ± 0.07	0.39 ± 0.02	0.43 ± 0.07	0.42 ± 0.02	0.46 ± 0.03	0.43 ± 0.02	0.42 ± 0.03	0.40 ± 0.01	0.44 ± 0.05	0.40 ± 0.02	0.41 ± 0.04
18:0	5.53 ± 0.27*	7.61 ± 0.61*	5.72 ± 0.30	7.55 ± 0.97	5.92 ± 0.26*	7.57 ± 0.61*	6.63 ± 0.48*	9.96 ± 1.09*	6.38 ± 0.10	8.28 ± 1.15	6.84 ± 0.22	8.81 ± 1.52	6.69 ± 0.13	9.53 ± 1.35
19:0	0.09 ± 0.01*	0.28 ± 0.09*	0.10 ± 0.01	0.20 ± 0.05	0.10 ± 0.01*	0.21 ± 0.06*	0.10 ± 0.01*	0.21 ± 0.04*	0.09 ± 0.01*	0.15 ± 0.03*	0.11 ± 0.01*	0.21 ± 0.03*	0.09 ± 0.01*	0.19 ± 0.03*
20:0	0.15 ± 0.01*	0.43 ± 0.10*	0.19 ± 0.02*	0.39 ± 0.06*	0.20 ± 0.01*	0.42 ± 0.06*	0.19 ± 0.02*	0.38 ± 0.05*	0.17 ± 0.01*	0.29 ± 0.06*	0.23 ± 0.01*	0.46 ± 0.05*	0.20 ± 0.02*	0.38 ± 0.05*
22:0	0.04 ± 0.01	0.23 ± 0.10	0.04 ± 0.01*	0.17 ± 0.05*	0.04 ± < 0.01*	0.25 ± 0.11*	0.07 ± 0.03*	0.22 ± 0.06*	0.04 ± < 0.01	0.15 ± 0.08	0.05 ± < 0.01*	0.28 ± 0.11*	0.04 ± < 0.01*	0.22 ± 0.09*
24:0	0.03 ± 0.01	0.37 ± 0.22	0.03 ± < 0.01	0.22 ± 0.11	0.02 ± < 0.01*	0.53 ± 0.28*	0.04 ± 0.02*	0.24 ± 0.09*	0.02 ± < 0.01	0.12 ± 0.08	0.02 ± < 0.01*	0.23 ± 0.12*	0.02 ± < 0.01*	0.17 ± 0.09*
Σ:0	37.34 ± 1.35*	33.78 ± 0.93*	35.39 ± 2.05	33.11 ± 0.80	36.95 ± 1.70	34.23 ± 0.91	38.09 ± 1.24	37.05 ± 0.85	36.95 ± 1.08	35.31 ± 0.72	37.09 ± 1.29*	32.22 ± 1.55*	36.47 ± 1.90	34.33 ± 0.76
14:1n-5	0.225 ± 0.032	0.320 ± 0.079	0.213 ± 0.031	0.373 ± 0.061	0.195 ± 0.020	0.339 ± 0.071	0.155 ± 0.017*	0.264 ± 0.041*	0.124 ± 0.006	0.206 ± 0.040	0.139 ± 0.013	0.230 ± 0.046	0.139 ± 0.016	0.218 ± 0.042
16:1n-9	0.548 ± 0.019	0.615 ± 0.033	0.520 ± 0.017	0.572 ± 0.024	0.491 ± 0.017*	0.581 ± 0.023*	0.494 ± 0.021	0.530 ± 0.030	0.528 ± 0.019	0.550 ± 0.025	0.511 ± 0.011	0.590 ± 0.043	0.511 ± 0.029	0.562 ± 0.049
16:1n-7	4.539 ± 0.410*	2.277 ± 0.320*	4.620 ± 0.498*	2.782 ± 0.428*	4.287 ± 0.393*	2.370 ± 0.278*	3.744 ± 0.293*	2.093 ± 0.300*	3.651 ± 0.138*	2.510 ± 0.316*	3.432 ± 0.190*	1.555 ± 0.220*	3.554 ± 0.269*	1.796 ± 0.300*
17:1n-8	0.201 ± 0.015	0.192 ± 0.050	0.191 ± 0.021	0.205 ± 0.040	0.184 ± 0.017	0.216 ± 0.073	0.170 ± 0.013	0.161 ± 0.016	0.172 ± 0.008	0.156 ± 0.011	0.154 ± 0.012	0.144 ± 0.024	0.163 ± 0.015	0.135 ± 0.023
18:1n-9	28.68 ± 1.27	25.96 ± 2.98	29.64 ± 2.20	26.81 ± 2.18	28.47 ± 1.61	26.87 ± 2.21	27.60 ± 1.53	23.96 ± 1.85	29.31 ± 1.30	27.70 ± 1.88	28.48 ± 1.40	26.08 ± 2.16	29.37 ± 2.32	26.37 ± 2.10
18:1n-7	2.548 ± 0.112	2.432 ± 0.043	2.523 ± 0.150	2.333 ± 0.070	2.513 ± 0.134	2.431 ± 0.049	2.517 ± 0.120	2.534 ± 0.057	2.587 ± 0.122	2.465 ± 0.100	2.506 ± 0.096	2.419 ± 0.083	2.530 ± 0.118	2.363 ± 0.099
20:1n-11	1.064 ± 0.069*	1.807 ± 0.268*	1.170 ± 0.121*	2.261 ± 0.233*	1.155 ± 0.074*	2.000 ± 0.212*	1.178 ± 0.108*	1.721 ± 0.144*	1.203 ± 0.098*	1.831 ± 0.203*	1.267 ± 0.056*	2.970 ± 0.304*	1.369 ± 0.134*	2.369 ± 0.236*
20:1n-9	2.253 ± 0.161*	3.226 ± 0.444*	2.595 ± 0.172*	4.039 ± 0.249*	2.660 ± 0.137*	3.588 ± 0.370*	2.435 ± 0.236	2.973 ± 0.258	2.647 ± 0.262	3.218 ± 0.253	2.930 ± 0.232*	4.364 ± 0.344*	3.095 ± 0.413	3.767 ± 0.285
22:1n-11	0.872 ± 0.055*	1.375 ± 0.094*	1.231 ± 0.123*	2.114 ± 0.219*	1.282 ± 0.088*	1.809 ± 0.176*	1.187 ± 0.100	1.518 ± 0.143	1.268 ± 0.183	1.576 ± 0.274	1.452 ± 0.112*	2.190 ± 0.228*	1.537 ± 0.135	2.001 ± 0.185
22:1n-9	0.143 ± 0.008*	0.358 ± 0.073*	0.180 ± 0.021*	0.459 ± 0.121*	0.182 ± 0.012*	0.350 ± 0.030*	0.161 ± 0.012*	0.278 ± 0.026*	0.167 ± 0.016	0.271 ± 0.065	0.202 ± 0.014*	0.375 ± 0.051*	0.191 ± 0.012*	0.360 ± 0.040*
22:1n-7	0.030 ± 0.003*	0.155 ± 0.074*	0.031 ± 0.006	0.086 ± 0.024	0.029 ± 0.003	0.119 ± 0.051	0.030 ± 0.004*	0.062 ± 0.012*	0.023 ± 0.002	0.054 ± 0.023	0.029 ± 0.004*	0.079 ± 0.028*	0.028 ± 0.003*	0.063 ± 0.014*
Σ:1	42.06 ± 1.83	41.62 ± 2.51	43.88 ± 2.90	44.28 ± 1.56	42.41 ± 2.24	43.14 ± 2.00	40.66 ± 2.12	38.18 ± 2.08	42.58 ± 1.82	42.09 ± 1.41	42.07 ± 1.93	43.13 ± 2.12	43.41 ± 3.07	41.90 ± 2.13
Δ9-DI	1.09 ± 0.10	1.07 ± 0.09	1.10 ± 0.14	1.13 ± 0.08	1.10 ± 0.14	1.10 ± 0.07	1.00 ± 0.09	0.89 ± 0.07	1.08 ± 0.08	1.05 ± 0.07	1.04 ± 0.09	1.10 ± 0.08	1.09 ± 0.14	1.02 ± 0.08

[a]An asterisk (*) indicates a significant difference between the fed and the fasted animals (*t*-test, Mann–Whitney U test, $P < 0.05$). The sums include also minor FA not presented in the table. For abbreviations see Table 1.

TABLE 3
Effects of Fasting on the Composition of PUFA (mol%) in Adipose Tissues of the American Marten[a] (mean ± SE)

	Scapular sc fat		Rump sc fat		Ventral sc fat		Mesenteric fat		Omental fat		Retroperitoneal fat		Diaphragmatic fat	
FA	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted	Fed	Fasted
18:2n-6	13.28 ± 0.35	13.25 ± 0.63	13.69 ± 0.31	13.52 ± 0.39	13.65 ± 0.21	12.93 ± 0.59	13.36 ± 0.31	12.47 ± 0.41	13.36 ± 0.25	13.65 ± 0.31	14.29 ± 0.37	14.81 ± 0.35	13.66 ± 0.42	14.40 ± 0.28
Σ:2	13.88 ± 0.34	14.27 ± 0.38	14.30 ± 0.29	14.28 ± 0.31	14.23 ± 0.20	13.78 ± 0.42	13.92 ± 0.31	13.21 ± 0.35	13.93 ± 0.25	14.26 ± 0.28	14.82 ± 0.38	15.38 ± 0.37	14.19 ± 0.43	15.05 ± 0.29
18:3n-6	0.138 ± 0.007	0.189 ± 0.058	0.138 ± 0.013	0.117 ± 0.019	0.135 ± 0.008	0.159 ± 0.058	0.124 ± 0.005	0.120 ± 0.014	0.123 ± 0.007*	0.098 ± 0.006*	0.129 ± 0.007*	0.090 ± 0.011*	0.125 ± 0.015	0.100 ± 0.005
18:3n-3	0.907 ± 0.041*	0.622 ± 0.054*	0.923 ± 0.058*	0.572 ± 0.039*	0.906 ± 0.042*	0.567 ± 0.046*	0.912 ± 0.049*	0.553 ± 0.065*	0.904 ± 0.052*	0.670 ± 0.069*	0.890 ± 0.054*	0.419 ± 0.040*	0.853 ± 0.095*	0.533 ± 0.048*
20:3n-6	0.170 ± 0.010*	0.351 ± 0.085*	0.183 ± 0.013	0.332 ± 0.080	0.176 ± 0.008	0.302 ± 0.067	0.200 ± 0.035*	0.444 ± 0.084*	0.164 ± 0.008	0.272 ± 0.061	0.186 ± 0.011*	0.389 ± 0.088*	0.179 ± 0.006*	0.319 ± 0.066*
20:3n-3	0.045 ± 0.004	0.179 ± 0.093	0.038 ± 0.003	0.072 ± 0.024	0.038 ± 0.002	0.149 ± 0.091	0.040 ± 0.004	0.073 ± 0.014	0.040 ± 0.003	0.061 ± 0.017	0.036 ± 0.003	0.069 ± 0.018	0.037 ± 0.006	0.055 ± 0.014
Σ:3	1.259 ± 0.047	1.341 ± 0.271	1.282 ± 0.080	1.093 ± 0.107	1.253 ± 0.053	1.177 ± 0.220	1.276 ± 0.079	1.191 ± 0.079	1.231 ± 0.063	1.101 ± 0.058	1.239 ± 0.065	0.967 ± 0.104	1.193 ± 0.121	1.006 ± 0.083
18:4n-3	0.294 ± 0.023	0.267 ± 0.071	0.280 ± 0.038	0.220 ± 0.030	0.285 ± 0.024	0.252 ± 0.078	0.288 ± 0.025*	0.195 ± 0.025*	0.307 ± 0.031	0.237 ± 0.029	0.252 ± 0.018*	0.131 ± 0.020*	0.256 ± 0.049	0.185 ± 0.035
20:4n-6	0.473 ± 0.040	1.532 ± 0.713	0.429 ± 0.050	1.373 ± 0.593	0.427 ± 0.033	1.340 ± 0.580	0.793 ± 0.353*	3.070 ± 0.889*	0.414 ± 0.038	1.475 ± 0.737	0.411 ± 0.036	2.486 ± 1.024	0.391 ± 0.062	1.805 ± 0.898
Σ:4	1.176 ± 0.082	2.963 ± 1.226	1.104 ± 0.124	2.381 ± 0.807	1.097 ± 0.083	2.549 ± 0.975	1.523 ± 0.419*	4.265 ± 1.062*	1.099 ± 0.098	2.352 ± 0.912	1.050 ± 0.078	3.387 ± 1.180	1.011 ± 0.157	2.705 ± 1.034
20:5n-3	0.714 ± 0.081	0.935 ± 0.478	0.633 ± 0.107	0.624 ± 0.201	0.586 ± 0.065	0.737 ± 0.326	0.822 ± 0.204	1.050 ± 0.255	0.658 ± 0.070	0.703 ± 0.247	0.491 ± 0.049	0.857 ± 0.341	0.483 ± 0.098	0.617 ± 0.255
22:5n-3	0.700 ± 0.041*	1.244 ± 0.294*	0.694 ± 0.069	1.051 ± 0.133	0.690 ± 0.051*	1.101 ± 0.174*	0.765 ± 0.079*	1.353 ± 0.206*	0.694 ± 0.055	1.001 ± 0.149	0.667 ± 0.045*	1.059 ± 0.130*	0.676 ± 0.094*	1.102 ± 0.117*
Σ:5	1.691 ± 0.130	3.016 ± 1.097	1.576 ± 0.206	2.229 ± 0.460	1.528 ± 0.133	2.455 ± 0.720	1.852 ± 0.303	2.858 ± 0.485	1.599 ± 0.148	2.080 ± 0.465	1.408 ± 0.113	2.341 ± 0.540	1.388 ± 0.233	2.158 ± 0.411
22:6n-3	2.594 ± 0.234	3.013 ± 0.459	2.470 ± 0.384	2.623 ± 0.203	2.539 ± 0.284	2.680 ± 0.257	2.673 ± 0.281	3.245 ± 0.282	2.606 ± 0.311	2.805 ± 0.190	2.318 ± 0.245	2.570 ± 0.362	2.334 ± 0.505	2.854 ± 0.202
Σ PUFA	20.60 ± 0.69	24.60 ± 2.83	20.73 ± 0.98	22.61 ± 1.46	20.64 ± 0.70	22.64 ± 1.89	21.25 ± 1.23	24.77 ± 1.61	20.46 ± 0.83	22.60 ± 1.46	20.84 ± 0.81	24.64 ± 2.43	20.12 ± 1.37	23.77 ± 1.81
Σ VLCFA	0.117 ± 0.021	0.976 ± 0.511	0.108 ± 0.012	0.669 ± 0.307	0.107 ± 0.009	1.103 ± 0.514	0.158 ± 0.050*	0.794 ± 0.251*	0.081 ± 0.007	0.463 ± 0.262	0.107 ± 0.010	0.796 ± 0.343	0.099 ± 0.013	0.635 ± 0.300
Σ n-6 PUFA	14.56 ± 0.40*	16.80 ± 0.87*	14.95 ± 0.42	16.39 ± 0.72	14.89 ± 0.28	15.85 ± 0.54	15.05 ± 0.70	17.41 ± 0.90	14.54 ± 0.33	16.36 ± 0.83	15.55 ± 0.45	18.86 ± 1.52	14.84 ± 0.55	17.65 ± 1.17
Σ n-3 PUFA	5.54 ± 0.41	6.94 ± 1.65	5.31 ± 0.67	5.64 ± 0.69	5.30 ± 0.47	6.11 ± 1.19	5.77 ± 0.61	6.85 ± 0.72	5.48 ± 0.53	5.79 ± 0.62	4.90 ± 0.41	5.43 ± 0.90	4.87 ± 0.86	5.68 ± 0.61
n-3/n-6	0.38 ± 0.03	0.39 ± 0.07	0.35 ± 0.04	0.34 ± 0.03	0.35 ± 0.03	0.38 ± 0.06	0.38 ± 0.03	0.39 ± 0.03	0.37 ± 0.03	0.35 ± 0.02	0.31 ± 0.02	0.28 ± 0.02	0.32 ± 0.05	0.32 ± 0.02
UFA/SFA	1.70 ± 0.12	1.98 ± 0.08	1.87 ± 0.19	2.03 ± 0.07	1.75 ± 0.16	1.94 ± 0.08	1.64 ± 0.10	1.71 ± 0.06	1.72 ± 0.09	1.84 ± 0.06	1.72 ± 0.11	2.16 ± 0.17	1.77 ± 0.16	1.92 ± 0.06
DBI	0.51 ± 0.02	0.51 ± 0.02	0.52 ± 0.03	0.53 ± 0.01	0.51 ± 0.02	0.52 ± 0.02	0.49 ± 0.02	0.47 ± 0.02	0.51 ± 0.02	0.51 ± 0.01	0.51 ± 0.02	0.53 ± 0.02	0.52 ± 0.03	0.51 ± 0.02
TACL	17.25 ± 0.05*	17.53 ± 0.07*	17.34 ± 0.05	17.55 ± 0.08	17.31 ± 0.04*	17.55 ± 0.07*	17.33 ± 0.05*	17.56 ± 0.07*	17.37 ± 0.04	17.53 ± 0.09	17.38 ± 0.04*	17.74 ± 0.10*	17.40 ± 0.07	17.65 ± 0.08

[a]An asterisk (*) indicates a significant difference between the fed and the fasted animals (*t*-test, Mann–Whitney U test, $P < 0.05$). For abbreviations see Table 1. The sums include also minor FA not presented in the table.

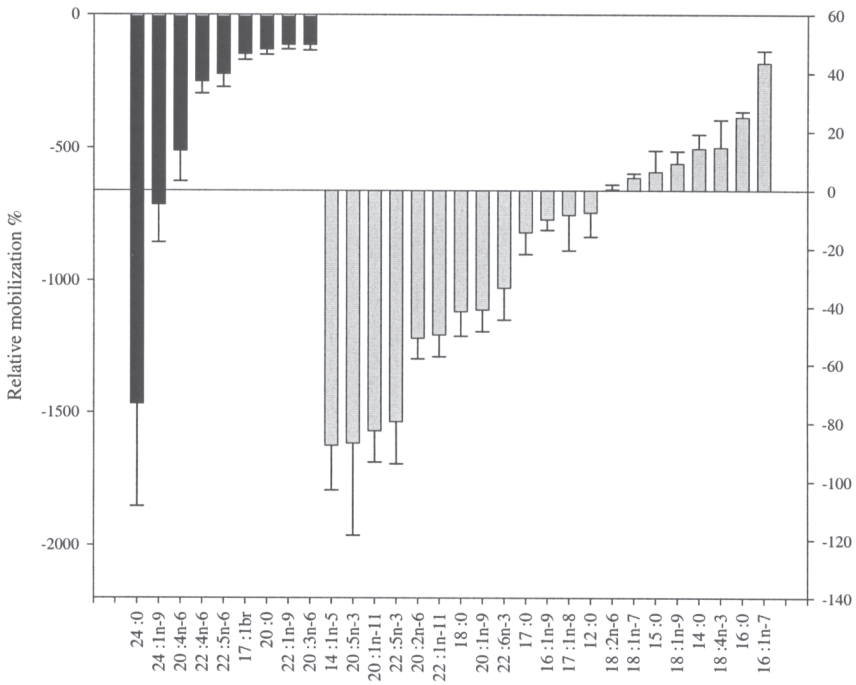

FIG. 1. *In vivo* relative mobilization of the most abundant FA in pooled adipose tissues of the American marten fasted for 2 d (mean + SE). Positive (+) values indicate that the proportion of a FA is lower compared with the fed control group, and negative (–) values signify that the proportion of a FA has increased compared with the fed control group. Black bars are plotted against the left Y-axis and gray bars against the right Y-axis.

MUFA, and, in particular, 2n-PUFA increased, while the proportions of 5n-PUFA decreased and the total percentage of the VLCFA increased. In the liver, the total proportion of SFA, 3n-, and 5n-PUFA was lower in the fasted animals. After 2 d of fasting, most FA were highly preserved in the fat depots (Fig. 1). The most important FA that had high relative mobilization were 16:1n-7, 16:0, 18:4n-3, and 14:0, whereas several long-chain MUFA and PUFA, such as 24:1n-9 and 20:4n-6, had mostly low relative mobilization, along with 14:1n-5, 17:0, 18:0, 20:0, and 24:0. Relative mobilization did not differ between the various iab and sc depots.

Relative mobilization of SFA correlated negatively with the chain length when all trunk WAT were analyzed as a whole (r_s = –0.327, $P < 0.01$; Fig. 2a). The same was observed in the n-9 MUFA (r_s = –0.350, $P < 0.01$; Fig. 2b) but not in the n-5, n-7, or n-11 MUFA. The influence of chain length on the relative mobilization of PUFA was tested by comparing PUFA with the same degree of unsaturation and position of the first double bond but with a different chain length. The difference was statistically significant in six out of eight pairs (16:2n-4 vs. 18:2n-4; 18:2n-6 vs. 20:2n-6; 18:3n-6 vs. 20:3n-6; 18:3n-3 vs. 20:3n-3; 18:4n-3 vs. 20:4n-3; and 20:4n-3 vs. 22:4n-3) in the way that the PUFA with the longer chain length had a lower mobilization rate (*t*-test, $P < 0.05$).

When SFA and corresponding MUFA with the same chain length were compared with each other, relative mobilization increased with Δ9-desaturation in four out of seven cases (16:0 vs. 16:1n-7; 18:0 vs. 18:1n-9; 19:0 vs. 19:1n-10, and 20:0 vs. 20:1n-11, *t*-test, $P < 0.05$; Fig. 2c). The influence of unsaturation on relative mobilization of PUFA was investigated by comparing PUFA with the same chain length and position of the first double bond but with a different double bond number. The difference was significant in three out of six pairs (18:3n-3 vs. 18:4n-3; 20:2n-6 vs. 20:3n-6; 20:3n-6 vs. 20:4n-6; Fig. 2d) in the way that the PUFA with the higher number of double bonds had the lower relative mobilization rate (*t*-test, $P < 0.05$).

The influence of positional isomerism on the relative mobilization of MUFA was tested by comparing MUFA of the same chain length but different position of the double bond. The difference was statistically significant in five out of seven pairs (*t*-test, $P < 0.05$) in the way that the MUFA with the double bond closer to the methyl end of the molecule had a lower (18:1n-5 vs. 18:1n-7; 20:1n-9 vs. 20:1n-11; and 22:1n-9 vs. 22:1n-11) or a higher mobilization rate (14:1n-7 vs. 14:1n-9 and 16:1n-7 vs. 16:1n-9). When comparing PUFA with the same chain length and unsaturation but with a different position of the first double bond, the difference was statistically significant in four out of six pairs (*t*-test, $P < 0.05$) in the way that the PUFA with the first double bond closer to the methyl end of the molecule had a lower (18:3n-3 vs. 18:3n-6; 18:2n-6 vs. 18:2n-7; and 22:5n-3 vs. 22:5n-6) or a higher mobilization rate (20:4n-3 vs. 20:4n-6).

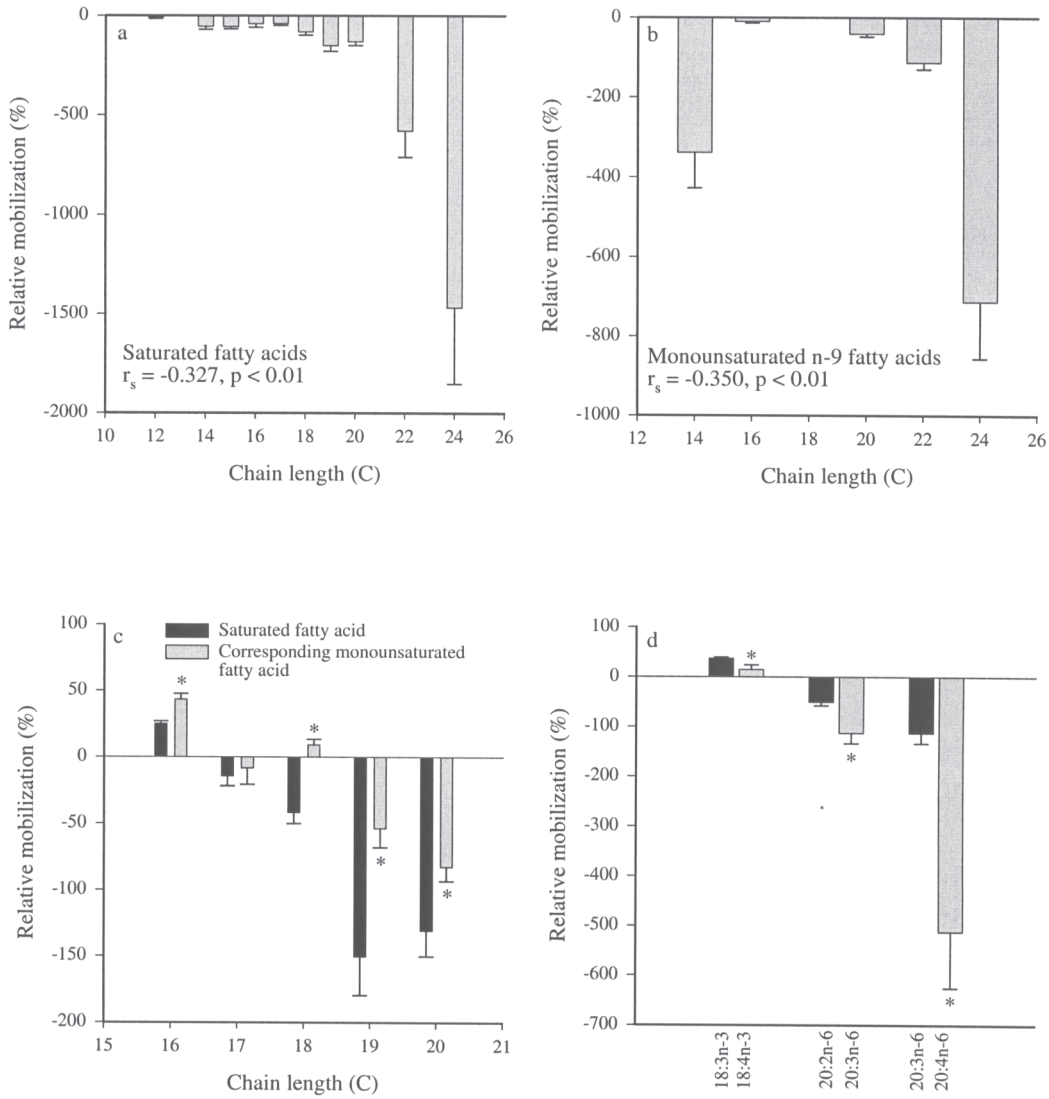

FIG. 2. Effects of FA structure on relative mobilization in the American marten after 2 d of fasting (all trunk white adipose tissues analyzed as a whole; mean + SE). (a) Relative mobilization of saturated FA of different carbon chain length. (b) Relative mobilization of n-9 monounsaturated FA of different carbon chain length. (c) The influence of Δ9-desaturation on relative mobilization. * = Significant difference in relative mobilization between saturated and monounsaturated FA (*t*-test, $P < 0.05$). (d) Effect of double bond number on relative mobilization of selected PUFA. * = Significant difference in relative mobilization between PUFA with different degrees of unsaturation (*t*-test, $P < 0.05$).

DISCUSSION

Body fat content and rate of weight loss. The rate of BM loss in the fasted American marten was 13.4% or 6.7% d^{-1}. This is slightly higher than the BM loss of 4.8% d^{-1} observed previously after a 5-d fasting period (12). At the same time, the BMI of the fasted marten of this study decreased by 18.5%. The total fat percentage of the marten was very low, approximately 2.7% for the fed animals and only a little more than 2% for the fasted animals. The data of the fed control animals fit quite well the previous report of Buskirk and Harlow (11). They measured a 2.4% body fat content in skinned American marten in Alaska, whereas in Wyoming the whole body fat content was approximately 5.6% in winter. The rate of BM loss in the marten was relatively high compared with a close relative, the farmed sable, which lost about 16% or 4.0% d^{-1} of its BM during a 4-d wintertime fasting period (Mustonen, A.-M., Puukka, M., Saarela, S., Paakkonen, T., Aho, J., and Nieminen, P., unpublished data). The sable had an 8.0% body fat content. The body fat percentage of the captive marten of this study was even more different from the farmed American mink, which can have a body fat content as high as 35–38% in the winter (15). Fasted mink lose weight at a rate of approximately 3.0% after a 2-d fasting period, which is about 4.5 times less than the weight loss rate of the marten was.

The smaller initial body fat percentage compared with the sable or the mink could be an explanation of the more rapid weight loss of the marten. Marten have been previously fasted for 5 d with fat as the principal source of metabolic energy (12). Yet the use of proteins is already quite significant at this point of fasting. It is conceivable that some body proteins could have been lost during the fasting procedure of the present study, as the total BM of the fasted marten decreased by 113 g, of which fat accounted for approximately 8.2 g. A major part of the BM loss probably consisted of intestinal contents, but also body proteins and carbohydrates could have contributed to the observed BM loss. However, plasma urea and ammonia levels as well as plasma, liver, and muscle protein concentrations remained stable during fasting while the liver, muscle, and kidney glycogen stores decreased (Nieminen, P., Rouvinen-Watt, K., and Mustonen, A.-M., unpublished data). These data indicate that the marten were still within phase II of fasting at the end of the experiment.

As an additional result, the clearly positive correlation between the BMI and the total fat mass or the body fat percentage indicates that the BMI can be used as an accurate and easily measured tool to approximate the body condition and fat content of American marten. To determine the condition of an individual marten, this can be supplemented by measuring the om fat mass (22). In fact, the correlation between the calculated BMI and the different fat depots was the most significant between the BMI and the om fat mass ($r_s = 0.828$, $P < 0.01$). The observation that the marten in the fasted group were physically active, many of them exhibiting stereotypical behavior and signs of stress, may be quite relevant to their rapid rate of body mass loss. This is most likely due to increased energy expenditure caused by accelerated locomotor activity as observed previously in fasted mink (23). In a similar manner, it has been observed that physical activity increases in the least weasel (*Mustela nivalis*) due to food deprivation (24).

Site-specific FA composition of the American marten. Generally, the FA composition in the sc and iab depots of the American marten was very similar to previous findings on other mustelids, the sable and the mink (25,26; Nieminen, P., and Mustonen, A.-M., unpublished data; Nieminen, P., Käkelä, R., Pyykönen, T., and Mustonen, A.-M., unpublished data). The most abundant FA in the fat depots of the marten were 14:0, 16:0, 18:0, 16:1n-7, 18:1n-9, and 18:2n-6. The proportions of total MUFA and PUFA in the trunk fat depots (42–43% and 22–23%, respectively) were closer to those observed previously in the farmed sable (40–45% and 20–25%) than to those in the farmed mink (50–55% and 10%). In this respect, the American marten is very similar to its Siberian relative, the sable, wheras both differ from the more distantly related mink. However, it must be recalled that the FA composition of the diets affecting the tissue FA percentages was probably dissimilar between the species of these experiments and could have caused some of the observed differences.

Proportions of MUFA and PUFA were much higher in the extremities than in the trunk of the marten. This was especially evident in the tip of the tail, with many n-3 PUFA, such as 20:3n-3, 20:5n-3, and 22:6n-3, in higher proportions than in the trunk. Furthermore, there was a simultaneous increase in the sum of n-3 PUFA in all the extremity tissues. The longer-chain 20- and 22-carbon PUFA were detected at higher proportions in the paws. In addition, the indices of unsaturation, the Δ9-DI, DBI and UFA/SFA ratio, were higher in the extremities, especially in the tail tip.

Previously, the FA composition of the extremities of mustelids has been studied in the mink and the sable (Mustonen, A.-M., Käkelä, R., and Nieminen, P., unpublished data; Mustonen, A.-M., and Nieminen, P., unpublished data). In this respect, the American marten is quite similar to the mink, as both species have decreased proportions of SFA and increased desaturation in the periphery. The differences between the fat depots of the trunk and the extremities are less pronounced in the sable, yet sables also have increased proportions of n-3 PUFA and VLCFA in their peripheral tissues. In general, the m.p. of mammalian fats are approximately 30–40°C, whereas the least insulated parts of the body, such as paw pads and the tail tip, may cool significantly more, down to 0°C in some conditions. The higher proportion of UFA in the periphery is probably crucial to prevent the solidification of lipids to maintain the fluidity of cell membranes. In fact, similar FA gradients have been detected from other boreal and arctic mammalian species, such as the European otter (*Lutra lutra*; 27), the blue fox (*Alopex lagopus*; 26), and beavers (*Castor fiber* and *C. canadensis*; 28). For instance, the adipose depots under the footpads of the otter have significantly more MUFA than the fat tissues of the trunk (27). Also, in the American marten, this phenomenon must be taken as an adaptation to the cold winter environment the species experiences in its natural habitat.

Effects of food deprivation on the relative mobilization of FA. In the fat depots of the trunk, the 2-d fasting period induced significant changes in the FA composition. In the SFA the proportions of long-chain FAs, especially 18:0, 20:0, and 22:0, increased with very few exceptions in most of the WAT depots, whereas the proportion of 24:0 increased especially in the iab fat. Simultaneously, the proportions of 16:0 decreased in all the studied fat tissues. Furthermore, the percentages of 18:3n-3 decreased in both pooled sc and iab fats, and the proportion of 18:4n-3 decreased in the iab fat, whereas the percentages of many n-6 PUFA, such as 20:2n-6, 20:3n-6, 20:4n-6, 22:4n-6, and 22:5n-6 increased. This caused an elevation in the sum of n-6 PUFA in both pooled sc and iab fats. At the same time, the proportion of 22:6n-3, an important FA for biological membranes (29), was unaffected by fasting. The conversion of various n-3 PUFA into the biologically important 22:6n-3 can be an explanation to the stable proportion of 22:6n-3 despite of fasting.

An increase in the proportion n-6 PUFA would be considered undesirable from the point of view of the human cardiovascular system as it causes harmful alterations in eicosanoid production (30). As the proportions of n-3-derived prostaglandins and eicosanoids decrease, unwanted proinflammatory changes in the immune response as well as cardiac arrhythmias and increased platelet aggregation may ensue. However, despite

this general effect of fasting on n-6 PUFA, the effects of positional isomerism on the relative mobilization of PUFA were inconsistent and no definite conclusions on the effects of fasting on n-3 and n-6 PUFA can be drawn from these data. The apparent increase in the proportion of n-6 PUFA can be caused by the analysis of FA from total lipids. There could have been a relative increase in the proportion of membrane phospholipids in comparison with storage TAG during fasting in the marten with a low body fat content. For instance, the increased proportion of phospholipids can be an explanation for the observed increases in 18:0 and 20:4n-6 in the fasted animals.

After 2 d of fasting, most of the relatively abundant FA were preserved in the fat depots. The anatomically different adipose tissues of the marten were very similar in this respect, as no significant differences in the mobilization rates of individual FA were found between the different WAT depots. Likewise, rats (*Rattus norvegicus*; 31) do not experience fat depot-associated differences in relative mobilization. The FA that were preferentially mobilized by the fasted marten were 16:1n-7; short-chain SFA, especially 14:0 and 16:0; 18:1n-9; and, in some of the fat depots, particular n-3 PUFA (18:4n-3).

The structure of FA may partly dictate the selectivity of FA mobilization. In the case of the American marten, short-chain FA were more readily mobilized over long-chain FA in all FA classes (SFA, MUFA, and PUFA). Shorter FA molecules are hypothesized to be situated peripherally in lipid droplets and can thus be more easily accessible to lipases (32). As a result, the proportion of longer-chain FA increases as the shorter-chain FA are mobilized for energy production. The same could be observed in the negative correlation between relative mobilization and chain length in all the fat depots of the trunk: the longer the carbon chain, the more obvious the preservation of a FA in an adipose tissue depot.

For a particular chain length, relative mobilization of FA increases with the number of double bonds in the rat (31). The same could be observed in the marten, as the mobilization of MUFA was higher than that of their corresponding SFA in 71% of the studied cases. However, in PUFA the effect was the opposite, as relative mobilization decreased with the number of double bonds in 50% of the cases. In this study, the effects of positional isomerism on relative mobilization were quite vague. This suggests that relative mobilization of FA during fasting is not as straightforward in all mammalian species as suggested by previous *in vitro* (32) and *in vivo* studies (31).

Ecophysiological implications. According to Buskirk (22), the American marten has limited fat reserves in the winter (2.4% of skinned carcass) and the om fat mass is considered the best indicator of body energy content. This would indicate that marten do not have enough stored body fat available to fast for long periods when foraging is impossible, e.g., during severe weather. To cope with this, marten may use microhabitats to avoid extremely cold temperatures. Furthermore, Thompson (33) suggests that marten reduce energy loss during winter by reducing activity, by eating large prey, and by being active during the warmest part of the day.

Despite its very low body adiposity, the American marten has adaptations to withstand short periods of food deprivation encountered in nature especially in the winter. According to Buskirk (22), if a marten had a body fat content of 2.37%, approximately the same as in the fed marten of this study, it would take 70 h for the animal to metabolize its fat reserves completely, putting the marten of this experiment still within the phase II of fasting. In fact, the marten were able to mobilize all their principal adipose tissue depots of the trunk during food deprivation. The FA mobilized were almost the same in sc and iab fats, indicating that as a terrestrial species the American marten is not very dependent on sc fat for insulation and can use it as an energy reserve for intermittent fasting. The principal FA mobilized were relatively short-chain SFA (14:0 and 16:0) and MUFA (16:1n-7 and 18:1n-9), and in the case of the iab fat, n-3 PUFA, especially 18:3n-3 and 18:4n-3. In contrast to this, the FA composition of the extremities was very resistant to fasting and contained significantly more long-chain PUFA than the depots of the trunk. This is probably an adaptation to maintain cell membrane fluidity and prevent freezing and solidification of these parts of the body most susceptible to cooling and frostbite.

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