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Indices to estimate fat depots in American marten *Martes americana*

Jean-François Robitaille & Eric W. Cobb

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The relationships between fat depots and body fat content and between protein content and protein indices were examined in American marten *Martes americana* carcasses obtained from trappers in northeastern Ontario during the 1995/96 fur harvest season. Percent fat and percent protein did not differ significantly between sexes ($t = 0.45$ and 0.55 , $P = 0.66$ and 0.58 , respectively). Protein contents did not vary much among 42 individuals (range: 14-19%), and therefore we found no significant index of percent protein ($0.01 < r < 0.23$, $P > 0.05$, $N = 42$). In the development phase, percent fat (PFAT) was better predicted by six of the eight potential fat indices, and better predicted in females than in males ($N = 17$ and 18 , respectively), but the omentum dry mass (ODM) performed best with both sexes ($r^2 = 0.69$ and 0.80 males and females, respectively). During the test phase ($N = 18$ males, 22 females), estimated PFAT based on ODM (per sex) did not differ from observed percent fat in either males or in females (paired $t = 0.01$ and 1.28 ; $P = 0.99$ and 0.22 , respectively). The models slightly over-estimated the number of males and females of below average condition, which indicates that the models were conservative. The accuracy of the omentum dry mass fat depot appears adequate to detect changes of physical condition in harvested marten populations. The lack of variation in protein contents 1) indicates that most animals were near average protein level, possibly due to suitable habitat conditions and 2) prevented us from finding a protein index. We encourage the development of models where conditions (e.g. temperature regime, level of disturbance, carrying capacity) may be harsher for marten.

Key words: energetics, fat depots, index, marten, *Martes americana*

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With the advancement of second-growth forests in the landscapes of northern Ontario, there is growing concern for the welfare of old-growth specialist species such as American marten *Martes americana*. Under pre-

vailing fragmentation of mature forest patches, source-sink contrasts may emerge where many individuals are forced into suboptimal habitats, and this may have a negative effect on population viability (Pulliam 1988, Pul-

liam & Danielson 1991; but see Watkinson & Sutherland 1995). In patchy environments, the ability to assess physical condition would help detect source and sink effects. Furthermore, the development of efficient physical condition indices would be helpful where there is potential for large-scale studies of physical condition/habitat selection, such as northern Ontario, and where large numbers of carcasses are available from the fur industry over a large area (Bissonette & Broekhuizen 1995).

While the relationship between diet, body condition and reproductive success has been documented for many species (e.g. Reimers & Ringberg 1983; see Haufler & Servello 1994 for an overview), the determinants of fitness in martens, especially martens from northern regions, are largely unknown, and are complicated by mortality risk during winter, which is itself compounded by several specificities of marten natural history (Buskirk & Powell 1994). Martens remain active throughout the winter season, and because of their elongated body shape, they are particularly susceptible to heat losses during cold boreal winter days. Martens have relatively little subcutaneous fat for insulation, and little fat overall (Buskirk & Harlow 1989) compared to other small to medium-sized carnivores (Pond & Ramsay 1992). Because of small energy storage, short-term energy balance in martens is critical, even though martens likely reduce their activity during colder days (Robitaille & Baron 1987, Harlow 1994), reduce their body-core temperature at rest (Buskirk, Harlow & Forrest 1988, Harlow 1994), and utilize favourable subnivean micro-environments for resting (Buskirk et al. 1988). Suboptimal habitats (such as sinks) may offer suboptimal trophic opportunities. For martens, winter survival may depend on the few energy reserves available. Furthermore, sex and age differences in fat dynamics can appear due to source-sink-dispersal effects, thus requiring the development and testing of separate indices.

The leanness of martens presents in itself a technical challenge in detecting, using a fraction of fat or protein depots and the dynamics of condition in a given population. In the context of large-scale studies, the lack of definite macroscopic depots may hinder the predicting performance of a chosen index, thus requiring the processing of whole carcasses in labour-intensive fat extraction analyses. Because index must rely on soft, metabolic tissues, large sample sizes are likely to be necessary to dampen the statistical 'noise' due to marten's short-term condition fluctuations among fasting episodes, capture dates, seasons, habitat patchiness, and due to variable condition of carcasses obtained from remote areas (i.e. trap lines). In martens, subcutaneous deposits,

when present, are confined to the inguinal and under-arm regions, but often present in thin layers of variable extent which cannot be removed with consistency; macroscopic internal depots include almost solely stomach omenta (lesser and greater) and kidney mesentery; the latter may extend in the inguinal region and forward along the dorsal mesentery (Strickland & Douglas 1987, J-F. Robitaille, pers. obs.). Internal macroscopic fat depots are prominent over the subcutaneous fat layer (Buskirk & Harlow 1989) and are thus better candidates as indices. On the other hand, because martens apparently derive much energy from protein (Harlow & Buskirk 1991), the assessment of physical condition in martens should include protein analyses. Only the greater omentum (hereafter omentum) has been tested as an index of body fat contents in martens (Buskirk & Harlow 1989); the relationship between body mass and protein content in martens has not yet been investigated.

The objective of this study was to search for, develop and test a potential index of physical condition in martens for northern Ontario. Specifically, we elected to test the relationship 1) between total body fat as measured through whole-body fat extraction, and selected macroscopic fat depots, and 2) between body mass and protein content. The development of a comprehensive, reliable and practical condition index would facilitate the examination of marten fat dynamics at a landscape scale, thus enabling large-scale analyses required to detect habitats or populations at risk in management or conservation areas. Furthermore, a cost-efficient index would allow multi-scale analyses probably needed to detect ecological (e.g. source-sink) effects in medium-sized carnivores such as martens. Finally, a standardized index would enable a better understanding of marten energetics, one of its prominent life history traits (Harlow 1994).

Material and methods

Specimen collection

Skinned marten carcasses were volunteered from nine registered trap lines near Sudbury (46°30'N, 81°00'W; N = 37 carcasses) and Cochrane, Ontario (49°00'N, 81°00'W; N = 40) between 28 October and 19 February of the 1995/96 fur harvest season. The carcasses were kept in individual plastic bags and frozen (ca. -15°C) until time of dissection. Carcasses were thawed in random batches at 8°C or at room temperature, sexed and retained for this study if general condition was good (no apparent freeze burns, no missing portions from scavenging), which was the case for all specimens (N = 77)

in this study. Gastro-intestinal tracts were emptied, the carcass was weighed (skinned carcass mass, SCM) using a Sartorius_{TM} balance (± 0.01 g), and heads were removed for non-destructive studies (e.g. skull morphometry and aging), and for separate fat contents analyses (see below). Martens were aged as either juveniles (<12 months old) or adults (>18 months old) based primarily on pulp:cavity ratio measurements in canines and secondarily on temporal muscle coalescence (Poole, Matson, Strickland, Magoun, Graf & Dix 1994, Cobb 2000). The resulting sex/age samples were 18 juvenile and 21 adult males, 22 juvenile and 16 adult females. The effect of age was assumed to be secondary to that of sex size dimorphism. In both sexes, juveniles had attained adults' total length, tail length, and hind foot length, and only in males were juveniles significantly lighter than their adult counterpart (mean SCM ± 1 SE: males: juveniles 696 ± 15 g vs adults 796 ± 14 g; $F_{1,38} = 4.85$, $P < 0.001$; females: 500 ± 10 g vs adults 516 ± 12 g; $F_{1,41} = 1.03$, $P = 0.31$) and smaller neck circumference (105 ± 2 mm vs adults 113 ± 1 mm). The body mass difference in males was also observed with headless carcasses ($F_{1,38} = 3.54$, $P < 0.01$), suggesting that head mass was not solely responsible for body size differences.

Body lipid and protein extraction

The greater omentum, the perirenal fat depots and the liver were excised from all 77 marten carcasses. The headless carcasses, liver and fat depots were weighed

separately (± 0.01 g), dried to constant mass at 60–90°C, weighed again, and prepared for fat extraction (Kerr, Ankney & Millar 1982). Each dry (headless) carcass, liver and fat depot was ground to a fine homogenate using mortar and pestle, and blender. Three 20-g aliquots were taken from each homogenate and placed into pre-weighed 250-ml Erlenmeyer flasks containing 100 ml of petroleum ether, which removes storage, but not structural, lipids (Dobush, Ankney & Kremetz 1985). The flasks were agitated by hand periodically over 24 hours after which petroleum ether was decanted through a nylon mesh (sieve opening < 0.25 mm). The procedure was repeated until the ether in the flask was transparent, indicating that no more fat was extracted. For the first 32 martens, a MANOVA revealed no significant variability in percent fat among the three aliquots (Wilks' $\lambda = 0.87$, $F_{2,29} = 2.16$, $P = 0.13$), so they were further pooled for each marten. Percent body fat was calculated as per Dobush et al. (1985) based on dry tissue ratios, and further corrected to fresh mass using a 0.3 factor, assuming initial water content of 70% (Buskirk & Harlow 1989; Table 1).

In a separate analysis conducted to assess a possible bias in analyzing headless carcasses, lipids were extracted from the first 16 heads (of the 77 carcasses), and fat contents determined following the same procedure used with the headless carcasses. Percent fat estimated for the whole carcass (carcass and head) was not significantly different from percent fat measured in the headless carcass ($F_{1,15} = 2.02$, $P = 0.06$); the two variables were

Table 1. Variables used to estimate percent body fat and protein content in martens from the District of Sudbury, Ontario, Canada, collected between October 1995 and February 1996.

Variable	Abbreviation	Unit	Use	Description
Headless fresh mass	HFM	g	Reference for fat index; protein index	Wet mass of ingesta-free carcass, head removed for non-destructive studies
Headless dry mass	HDM	g	Reference for fat index; protein index	Dry mass of ingesta-free, headless carcass
Protein mass	PROT	g	Reference for protein levels	Protein mass = PPROT * HFM / 100
Percent protein	PPROT ^a	%	Reference for protein levels	(Total lean dry mass (g) of aliquots - ash mass (g)) / total lean dry mass (g) * 100 * 0.3
Percent fat	PFAT ^a	%	Reference for fat levels; protein index	Fat (homogenates + liver + omentum + perirenal) / HFM * 0.3
Omentum fresh mass	OFM	g	Fat index	Self-explanatory
Omentum fresh ratio	POFM	%	Fat index	OFM / HFM * 100
Omentum dry mass	ODM	g	Fat index	Self-explanatory
Omentum dry ratio	PODM	%	Fat index	ODM / HDM * 100
Perirenal fresh mass	PRFM	g	Fat index	Self-explanatory
Perirenal fresh mass	PPRFM	%	Fat index	PRFM / HFM * 100
Perirenal dry mass	PRDM	g	Fat index	Self-explanatory
Perirenal dry ratio	PPRDM	%	Fat index	PRDM / HDM * 100
Skinned carcass mass	SCM	g	Protein index	Initial carcass mass, head included, minus ingesta
Total body length	TBL	mm	Protein index	Linear measurement from nose to base of tail
Neck circumference	NC	mm	Protein index	Self-explanatory
Liver fresh mass	LFM	g	Protein index	Self-explanatory
Fresh liver ratio	PLFM	%	Protein index	LFM / HFM * 100
Liver dry mass	LDM	g	Protein index	Self-explanatory
Dry liver ratio	PLDM	%	Protein index	LDM / HDM * 100

^a The constant 0.3 accounts for an initial water content of 70% (Buskirk & Harlow 1989).

strongly correlated $r = 0.99$, $P < 0.0001$). We concluded that the use of headless carcasses did not bias our PFAT estimates.

For protein contents, three 10-g aliquots of lean dry homogenate (obtained from the previous fat extraction procedure) were obtained from the first 42 of the 77 martens (11 juvenile and nine adult males, and 12 juvenile and 10 adult females) and placed in pre-weighed 100-ml Erlenmeyer flasks, capped and heated at 500°C for six hours (Huot & Picard 1988). The residual ash was weighed and the amount of protein was estimated from the mass loss. A MANOVA revealed no significant variability among the three aliquots (Wilks $\lambda = 0.99$, $F_{3,39} = 0.15$, $P = 0.86$), so they were pooled for each animal. Percent protein (PPROT) and protein mass (PROTM) of a headless carcass was calculated as per Waterlow (1969; see Table 1).

Fat and protein analyses

Fourteen variables, including reference variables and candidate indices, were used to develop indices for fat levels (liver mass, omentum and perirenal fat depots and associated ratios) and for protein levels (liver fresh and dry mass and associated ratios; SCM; see Table 1). We analyzed candidate indices based on fresh masses of depots, by sex/age group to control for body size, and also used ratio variables corrected for body mass (%), as well as dry tissue masses (g) and their ratios (%) to control variability in water contents (see Table 1). Wherever appropriate, variables were normalized using either logarithmic transformations or truncations of outliers more than three standard deviations from the mean.

In order to construct a fat index, the marten sample of 77 was initially split into 1) a development set of 37 martens (seven juvenile and 12 adult males, 10 juvenile and eight adult females) to build a predictive function between each candidate index and known PFAT levels, and 2) a test set using the last 40 animals (10 juvenile and eight adult males, 12 juvenile and 10 adult females), which will allow assessing the performance of the developed function in predicting actual PFAT levels in an independent group of animals. In the development phase, Pearson correlations were initially used between PFAT and candidate indices and tested for significant differences using paired t-tests after Fisher's z-transformations (Kleinbaum, Kupper & Muller 1988) to select the test variables that better reflected variation in PFAT. Using selected variables, model functions were obtained from individual least squares linear regressions against PFAT. In the test phase ($N = 40$), predicted fat levels (EstPFAT) were obtained using the model functions, and compared with PFAT using paired t-test. The

frequency distributions of PFAT and EstPFAT were examined and compared. Unpaired t-tests and analyses of covariance (ANCOVA) were used to detect sex effects in the fat indices.

For protein analyses, the relationships of protein mass (PROT) and percent protein (PPROT) with PFAT, the liver fresh and dry masses (LFM, LDM) and percent (PLFM, PLDM), body mass (HFM, HDM, and SCM) were examined using another subset of our sample ($N = 20$ males and 22 females). Where necessary, variables were normalized using either logarithmic transformations, or truncations of outliers more than three standard deviations from the mean. Pearson correlations between protein mass and index variables were tested for significance and compared using two-tailed unpaired t-tests after Fisher's z-transformations; because percent protein (PPROT) could not be normalized, Spearman's rho was used. All statistical analyses were done using JMP version 3.2 (SAS 1995). Data are presented as means \pm standard error unless stated otherwise.

Results

Mean skinned carcass mass (SCM) of the male martens was significantly greater than that of females. Male SCM was 750 ± 13 g (range: 619-917 g, $N = 39$) and females 506 ± 8 g (range: 390-592 g, $N = 38$), respectively (Wilcoxon's $z = 7.42$; $P < 0.0001$). Within each sex/age group, body size variables (HFM and HDM) were normally distributed ($0.91 < W < 0.98$, $P > 0.05$). Fat contents (PFAT \pm SE) of martens ranged between 0.22 and 8.15% (mean: $2.75 \pm 0.17\%$, $N = 77$) and were normally distributed among adult males (mean: $2.61 \pm 0.25\%$) and among juvenile females (mean: $2.76 \pm 0.30\%$). Juvenile males and adult females had one outlier each (7.51 and 8.15%, respectively), and the medians of each cohort were 2.60 and 2.35% respectively (Table 2). We noted that there was a relatively high number of animals ($N = 10$) in the lower fat ranges, but all sex/age classes were represented in any interval (see

Table 2. Distribution of fat contents (PFAT; in %) in 77 martens collected in northern Ontario between October 1995 and February 1996.

PFAT (%)	Juvenile ♂♂	Adult ♂♂	Juvenile ♀♀	Adult ♀♀	Total
0-1	3	2	1	1	7
1-2	2	4	7	5	18
2-3	5	9	4	4	22
3-4	5	4	7	3	19
4-5	1	2	1	1	5
5-6	1	0	1	1	3
>6	1	0	1	1	3

Table 3. Univariate regression models relating total body fat (in %) various measurements of fat depots of 18 male and 17 female martens collected in northern Ontario between October 1995 and February 1996.

Independent variable	Sex	Intercept	SE	Slope	SE	R ²	F	P ^a
Omentum fresh mass (OFM)	♂	1.507	0.263	0.280	0.072	0.49	15.28	0.001
	♀	0.853	0.190	0.564	0.072	0.81	62.08	***
Omentum dry mass (ODM)	♂	1.360	0.202	0.603	0.102	0.69	35.09	***
	♀	1.085	0.171	1.045	0.136	0.80	58.79	***
Perirenal fresh mass (PRFM)	♂	2.075	0.394	0.195	0.203	0.05	0.92	0.350
	♀	0.607	0.467	1.434	0.419	0.44	11.74	0.004
Perirenal dry mass (PRDM)	♂	1.398	0.288	1.320	0.338	0.49	15.22	0.001
	♀	0.909	0.212	2.906	0.430	0.75	46.08	***
Percent omentum fresh mass (POFM)	♂	1.459	0.266	1.633	0.408	0.50	16.27	0.001
	♀	0.735	0.251	2.323	0.372	0.72	39.07	***
Percent omentum dry mass (PODM)	♂	1.453	0.221	0.991	0.199	0.61	24.70	***
	♀	0.927	0.188	1.441	0.189	0.80	58.42	***
Percent perirenal fresh mass (PPRFM)	♂	1.982	0.430	1.392	1.267	0.07	1.21	0.290
	♀	0.555	0.623	5.506	2.135	0.31	6.65	0.021
Percent perirenal dry mass (PPRDM)	♂	1.443	0.302	2.302	0.647	0.44	12.65	0.003
	♀	0.715	0.246	4.044	0.626	0.73	41.72	***

a ***: P < 0.001

Table 2). Fat contents did not differ significantly between sexes ($F_{2, 76} = 0.45$; $P = 0.66$) or among the sex/age classes ($F_{4, 73} = 0.17$; $P = 0.92$). In the development of indices, ages were pooled, but sexes were treated separately because of more probable body size and life strategy effects on fat dynamics.

In the development phase of a fat predictive function ($N = 37$), \log_{10} -transformed fat depot indices (OFM, POFM, ODM, PODM, PRDM, PPRDM, PRFM and PPRFM) were strongly correlated ($0.64 < r < 0.91$; $P < 0.0001$) with \log_{10} PFAT, and were thus retained for regression analyses (Table 3). In contrast, the liver variables LFM, PLFM, LDM and PLDM ($-0.07 < r < 0.47$; $ns < P < 0.05$) were discarded. Variance was homogeneous between PFAT and each index ($N = 37$), but the occurrence of two outliers (one juvenile male and one adult female) increased the variance explained by the regression model (E.W. Cobb, unpubl. data). The regression models were thus based on truncated data sets to approach homoscedasticity, although the inclusion of outliers did not change fits of regressions (Cobb 2000). We recognize that a valid condition index would be able to detect accurately lower as well as higher condition levels, and this is being tested here. Regressions using untransformed, truncated, data yielded better fits than otherwise, and was preferred for simplicity. Regression analyses were run on 18 males and 17 females.

PFAT was generally better predicted in females than in males, indicating that more unexplained variance exists in male fat depot allocation than in female (see Table 3). Furthermore, in all models generated, males had a smaller slope than females, indicating a relatively slower increase in internal fat depots than in PFAT. Among the eight fat indices, however (see Table 3), omental dry mass (ODM) performed best with both

males and females ($R^2 = 0.69$ and 0.80 , respectively), followed by PODM and PRDM.

In the test phase using 40 new individual martens, estimated percent fat (EstPFAT) was calculated using ODM, PODM and PRDM indices (per sex) and compared to actual PFAT values. PFATs ($N = 40$) averaged 2.93% (range: 0.22-6.51%) and were normally distributed (Shapiro-Wilk's $W = 0.97$; $P = 0.50$), but EstPFATs were not ($0.84 < W < 0.92$; $P < 0.001$). ODM EstPFAT averaged 2.88% (range: 1.27-8.53%), PODM EstPFAT averaged 2.75% (range: 1.11-7.82%), and PRDM EstPFAT averaged 3.20% (range: 1.35-7.39%). Paired t-test revealed no significant differences

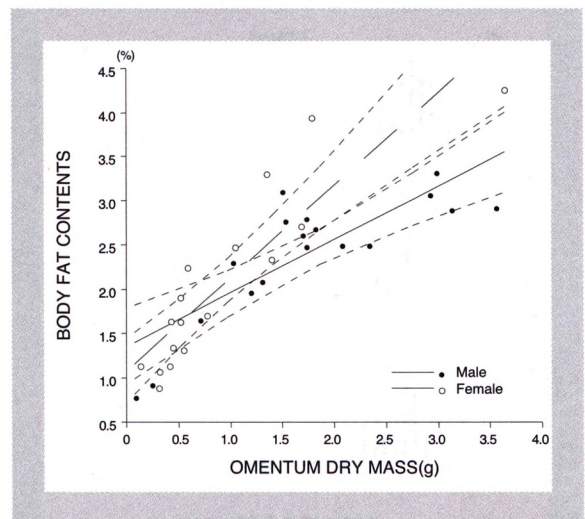


Figure 1. Relations between omentum dry mass (ODM; in g) and percent body fat (PFAT; in %) for 18 male and 17 female martens in northern Ontario, Canada, during October 1995 - February 1996. The slope for males (—; $Y_{\text{male}} = 0.603(\text{ODM}) + 1.360$) is smaller than for females (---; $Y_{\text{female}} = 1.045(\text{ODM}) + 1.085$).

between the means of ODM and PODM EstPFAT and PFAT, respectively ($F_{1,39} = 0.37$ and 1.28 ; $P = 0.72$ and 0.21 , respectively), but revealed a significant difference between PFAT and PRDM EstPFAT ($F_{1,39} = -2.41$, $P < 0.05$), indicating that PRDM overestimated fat contents more frequently than not.

We compared PFAT and EstPFATs for all 77 martens, sexes combined (but using separate ODM functions; Fig. 1). ODM, PODM or PRDM rendered average values (2.72, 2.62 and 3.00%, respectively) close to average PFAT (2.75%). However, upper ranges yielded by ODM and PRDM were higher (10.19 and 16.24%, respectively) than actual PFAT (8.15%), while the minimum fat contents yielded were higher (1.23 and 1.14%) than minimum PFAT (0.22%). Thus, all three indices failed to detect occurrence of lower fat contents for 10-12 animals. Nevertheless, based on ODM EstPFAT, more males (25 vs 19) and more females (27 vs 22) had fat level below the mean for their cohort (Fig. 2). Thus, ODM EstPFAT slightly overestimated the number of animals in below average condition.

Finally, it appears that the use of sex-dependent regression models was justified. In all eight models, males showed a different slope and intercept of the index relative to the amount of body fat. This trend suggests a different fat allocation strategy, where females show more variance in internal fat depots than males. We suggest that this is a body size effect.

Percent protein (PPROT ± 1 SE, $N = 42$) had a nor-

mal distribution in both males and females, with an average of $17.40 \pm 0.14\%$ and a narrow range (13.69-19.18%). PPROT did not differ significantly between sexes ($t = 0.55$, $P = 0.58$) or among the sex/age classes ($F = 1.41$, $P = 0.26$). As expected, PPROT was correlated with protein mass (PROT; $\rho = 0.52$, $P < 0.01$). However, it was not correlated with any of the possible indices: PFAT, SCM, HFM, HDM, LFM, LDM, PLFM or PLDM ($-0.04 < \text{Spearman's } r < 0.23$; $N = 42$). As expected, PROT was strongly correlated with skinned carcass mass (SCM) in both males and females (Pearson's $r = 0.78$ and 0.84 , respectively; $P < 0.0001$) reflecting dependence of protein contents on body size.

Discussion

Fat levels and indices

For obvious reasons, we could not validate ourselves the use of skinned, rather than whole, carcasses, but evidence supports this approach. First, professional trappers become quite skilled after the course taught by the Ontario Trapper's Association (K. Monk, pers.comm.), such that marten carcasses are prepared consistently and little or no subcutaneous fat is removed with the skin. Furthermore, in a separate study, Buskirk & Harlow (1989) showed that skin fat contents were proportional to those of the body. Marten carcasses volunteered by the fur industry offer a plentiful (and ethical) resource for large-scale wildlife studies and management, as long as skin can be omitted in physical condition assessment.

The use of headless carcasses and fat extraction procedure introduced little variability: we found non-significant variability in fat content among the three 100 ml extraction aliquots or between the head and body of each marten. Average fat content of our marten sample approximated that of martens from Alaska (2.4%); the departure of Wyoming data (mean: 4.6%) remains unexplained (Buskirk & Harlow 1989).

In the model-building phase, variance explained was relatively high despite limited sample sizes. One complication was the skewed frequency distributions for most fat variables: most male and female martens ranged low in fat values, while a few outlying fat content values were found in all sex/age groups. Models based on omentum dry mass predicted well even the higher fat levels of a few outliers present in the test group. By comparison, perirenal depots, especially fresh, performed poorly in predicting percent fat. On a technical note, perirenal depots are also harder to define at dissection (Buskirk & Harlow 1989; J-F. Robitaille, pers. obs.), and may con-

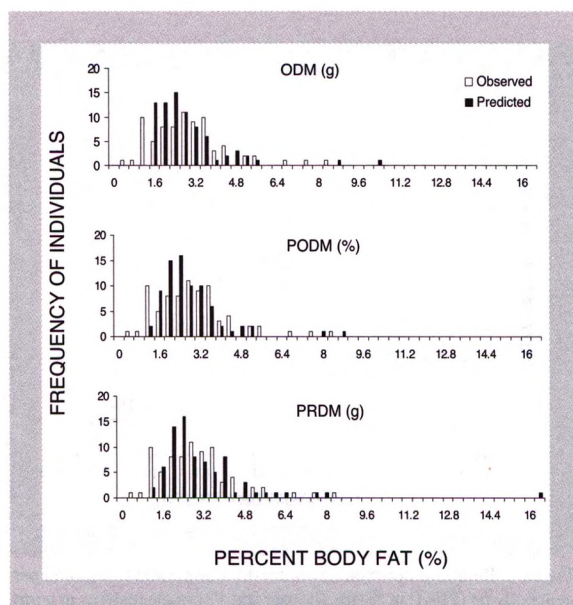


Figure 2. Distribution of estimated fat (EstPFAT) and actual body fat (PFAT; in %) in male and female martens combined, based on ODM(g), PODM (%) and PRDM (g).

tain more non-adipose tissue. Given these observations, we propose that omentum (preferably dry) is a relatively efficient index of fat contents of martens.

The potential of ODM for rendering a faithful portrayal of fat dynamics depends on the statistical parameters examined, thus the goals of the study. This study provides a sex-specific index, ODM, which allows detecting changes (e.g. temporal) in central fat contents values (e.g. mean). Here, we were able to detect lower fat values by focusing on the frequency distribution of the lower half of the population's fat range. This statistical approach slightly overestimates the number of animals in poorer condition, but allows detecting extreme low values. This obviously requires a minimum sample size, and a landscape-based sampling. The regression models tend to centralize values towards a normal distribution, and thus yield little information on extreme ranges (low and high) intrinsic to the actual fat distribution shown here, and its potential biological significance.

Differences between predicted fat and actual fat contents resulted in some mis-classifications of males or females from good to poor condition (as defined by the mean): 18% (seven of 39) of males and 13% (five of 38) of females. We consider that it is conservative and that it would not overestimate the physical condition in a population. Wherever the detection of less fit animals is critical (e.g. conservation purposes), our model will be able to detect lower trends in the allocation of fat in a marten population. Users would be encouraged to use the index on a comparative basis wherever possible.

Initial analyses indicated that fat levels were similar among age cohorts of the same sex, and there is no published evidence of an age effect on fat dynamics between juveniles and adults in martens. Martens have a relatively short life expectancy (especially in harvested populations) and an early age at sexual maturity. By late October (when martens are commercially trapped in Ontario), juveniles are close to adult size (Strickland & Douglas 1987, this paper). We assumed that martens of different ages within the same sex cohort experienced similar energetic constraints and had similar fat distributions that could be predicted by the same fat index. Also, we assumed that fat dynamics would be a function of body size, thus similar between juveniles and adults. Indeed, it appears strongly in this study that the relationship between a given fat depot and percent fat in the body is significantly different between the highly size-dimorphic martens. The use of two indices as proposed here (i.e. one per sex group) is considered an appropriate level of control over potential body-size related physiological and life history traits.

As expected, the liver variables proved to be relatively poor predictors of body fat contents since the liver is of little importance in fat storage (Spector 1956, Buskirk & Harlow 1989). Water content was an adequate index in other species (Virgl & Messier 1993), but in our analyses, fresh fat depots did not perform as well as their dried equivalent. This is probably a procedural limitation inherent to the use of commercial, rather than experimental animals: there is an inevitable variable degree of dehydration of carcasses between the times of capture, storage and post-mortem examination (Greer 1968; J-F. Robitaille, pers. obs.). We cannot dismiss the potential of water contents as a condition index in martens. Moreover, the use of dry tissues as condition indices is less straightforward than that of fresh masses, but appears necessary to reduce variability due to water content with trapped populations.

Compared to other mammals (Riney 1955, Lochmiller, Hellgren, Grant & Varner 1985, Torbit, Carpenter, Swift & Alldredge 1985, Litvaitis, Clark & Hunt 1986, Cothran, Chesser Smith & Johns 1987, Winstanley, Saunders & Buttemer 1998), martens are lean, and fat reserves may only reflect, short-term energy budgets rather than the long-term fitness of individuals (Harlow 1994). However, at the landscape level, the fitness of a population may depend on the proportion of healthy individuals that at any one time compose the population, and a latitudinal sampling approach might compensate for short-term, longitudinal effects. Thus, we suggest that the use of omental dry mass is valid in the context of landscape-scale studies on physical condition of martens as this may relate to disturbance levels, or habitat suitability.

Protein indices

During periods of high-energy demands, most mammals derive energy from fat and protein reserves, categorized into three general phases (Cahill 1970, Harlow & Buskirk 1991). In martens, protein catabolism during the second phase is greater than in other similar-sized mammals, and there is an early transition to a third terminal phase. In marten populations severely impacted by a lack of food, protein loss may occur, but in this study, and compared to fat dynamics, we failed to detect large variation in protein amounts in martens, and hence a significant index of relative (%) protein contents. Protein mass can be lost during fasting (Torbit et al. 1985, Harlow & Buskirk 1991), as well as water content, so a detectable change in the relative protein content (based on the analysis of reasonably small aliquots), may not be possible until near starvation (Waterlow 1969, Neuberger & Richards 1969, Bintz, Palmer, Mackin & Blanton 1979).

Given the technique used, our protein analyses did not account for inert or mobile forms and this may have obscured the relationship between fat levels and available protein energy reserves (Neuberger & Richards 1969). Nevertheless, mean percent protein of our martens approximated values found in rabbits *Oryctolagus cuniculus* and rats *Rattus rattus* (Munro & Fleck 1969), and except for one low outlying specimen, it appears that protein level in the marten was within a narrow range. This was not unexpected in our population that was kept below carrying capacity by commercial trapping. Whether protein levels are different in protected, high-density populations remains to be studied.

Conclusions

We are proposing that in the context of harvested marten populations of northern Ontario, changes in the physical condition of martens at the landscape level can be detected using a fat index based on omentum dry mass. Obviously, physical condition indices may vary among species (see above), so the model provided here must be restricted to martens. Furthermore, given the relatively narrow geographical range of the sample studied, we acknowledge the possibility that similar, but spatially-explicit models be required, especially given the possible effects of demography, population densities in unexploited populations, and temperature regimes. Given the satisfactory performance of our model, we encourage the development of other regional databases, for a better understanding of fat dynamics in martens.

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